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The Discovery of *Paramphistomum hiberniae* Willmott, 1950 and its Intermediate Host in the Channel Islands

By S. WILLMOTT, B.Sc., Ph.D. and F. R. N. PESTER

From investigations made by us from 1949 onwards, it has become apparent that paramphistomes are not as rare in cattle in the British Isles as had been previously supposed, the incidence in some areas being as high as 40 per cent. Although we have found a considerable number of infected animals at abattoirs at different times, the difficulties encountered in tracing these to their farms of origin were almost insuperable.

In the comparatively few cases which were traced by us, diligent searching of aquatic snails collected on the farms failed to reveal any snail naturally infected with paramphistomes: attempts at experimental infection of snails bred in the laboratory were also unsuccessful. For the infection experiments only snails of British origin were used.

Recently, through the kind offices of Mr. Nigel Sloan of the Cooper Research Station, adult paramphistomes were obtained from one of the Channel Island cows at a farm near Leighton Buzzard. Faecal examinations revealed that at least one other of these cattle was infected, whereas the home-bred beasts were negative. One of us (F. R. N. Pester) visited the Channel Island farm where these cattle had been bred and collected snails and cattle faeces.

The pasture where the cattle had been grazed yearly from April to November is marshy and at the time the snails were collected was under water. *Planorbis leucostoma* Millet (formerly *P. spirorbis* or *P. spirorbis* var. *leucostoma*) containing paramphistome rediae and cercariae were eventually found on the underside of the vegetation, both in the pasture itself and in a stream running through the fields. This same stream also ran through a neighbouring farm. Animals on both farms showed paramphistome eggs in the faeces. Some of the snails also emitted the cercariae which were ocellate, pigmented and without pharyngeal pouches; they encysted readily on indigenous aquatic plants and young oats, although they would not encyst on coarse grass.

The cercariae appear to be more heavily pigmented than those described by Brumpt in 1936 for *Paramphistomum cervi* from *Planorbis exustus* in Corsica, and those described by Szidat in the same year in his account of the life-history of *P. cervi* in Germany where the intermediate host is *Planorbis planorbis*. It appears possible from a comparison of these two accounts that the authors were not dealing with the same species and that *P. cervi* of Brumpt and *P. cervi* of Szidat are not identical. Unfortunately, Brumpt did not illustrate or describe the adults he obtained and those figured by Szidat are extremely young.

It is interesting to note that there is no previous record of these parasites in the Channel Islands although they had apparently been observed by a slaughterer in an abattoir there "a long time ago".

Experimental work is being continued. Encysted metacercariae have been fed to a bullock at the Winches Farm Field Station of the London School of Hygiene and Tropical Medicine at St. Albans.

SUMMARY.

Planorbis leucostoma Millet has been found to be a natural intermediate host for *Paramphistomum hiberniae* in the Channel Islands.

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Factors Influencing the Emergence of Larvae from Cysts of the Beet eelworm, *Heterodera schachtii* Schmidt

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The economic importance of root eelworms as pests is related to their numbers and rate of multiplication in the soil. A knowledge of the factors which govern population growth is desirable and this demands, basically, a study of the relationship between the eelworm and its environment. This paper deals with the effects of temperature, oxygen, saturation deficiency and soil moisture on the first phase of population development in the beet-eelworm (*Heterodera schachtii* Schmidt), namely the emergence of larvae from cysts. Fenwick (1951) has studied the influence of some physical conditions on larval emergence in the potato-root eelworm (*Heterodera rostochiensis* Woll.) but, because of the different characteristics of the two species, his approach to these problems was somewhat different from that adopted by the writer. One of the chief differences influencing the design of the experiments is the high larval emergence in water given by the beet eelworm, which enables some experiments to be conducted without the use of root diffusates.

The techniques for the assessment of larval emergence from cysts were simple. Four- or five-fold replication was employed with batches of 100 cysts per replicate. Larvae were counted in watch-glasses marked with concentric rings, a dilution of the larval suspension being employed where necessary. Diffusates were obtained by a method similar to that described by Fenwick (1949). Most experiments were repeated at least once and the results obtained agree closely with those given below.

TEMPERATURE.

Experiments on larval emergence in a series of constant temperatures showed that, of those temperatures tested, 25°C. was the optimum. The mean number of larvae emerging at this level was significantly higher than at 20°C. and 30°C., whilst emergence was almost nil at 10°C. and 35°C. The results, given in Fig. 1, support the findings of Baunacke (1922). In experiments on the effect of temperature on larval emergence of *H. rostochiensis*, Fenwick (1951) found that a temperature of 30°C. inhibited emergence; between 15°C. and 25°C., rise of temperature gave an increase in the rate of larval emergence.

Although it is useful to know the optimum constant temperature for larval emergence, it is clear that this condition does not prevail in the field, where temperature fluctuates. Bishop (1953) has shown that fluctuating temperature increases the rate of larval emergence from cysts of *H. rostochiensis*. An experiment was set up to see if fluctuating temperature had any influence on larval emergence in *H. schachtii*. Cysts in beet diffusate were subjected to six different daily treatments. The treatments and numbers of larvae emerging are given in Fig. 2. Larvae were counted at weekly intervals over a five-week period. The weekly temperature treatment at which maximum emergence occurred was 16 hours at 15°C. and eight hours at 24°C. per day for five days followed by two days at a constant temperature of 15°C.

OXYGEN.

The oxygen concentration of the soil water and soil atmosphere varies considerably with the type of soil, amount of biological activity, soil moisture, season, etc. (Baver, 1948). Therefore, the effect of oxygen concentration on larval emergence seems to be a factor worthy of investigation. Triffitt (1930) showed that the larvae of *H. rostochiensis* do not emerge in the absence of oxygen.

Cysts were placed in sealed tubes containing distilled water at different oxygen concentrations, replenishment of oxygen from the air being prevented. Oxygen concentrations were determined by Winkler's method. The larvae which had emerged during seven days

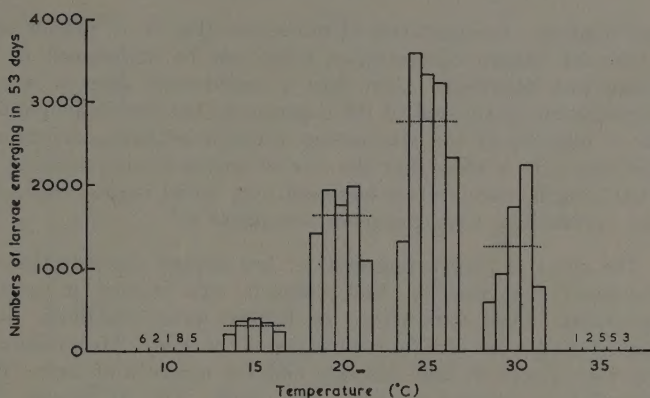


Fig. 1.—Effect of temperature on larval emergence. The horizontal dotted lines indicate the mean of five replicates. At 10°C. and 35°C. actual numbers of larvae per replicate are given.

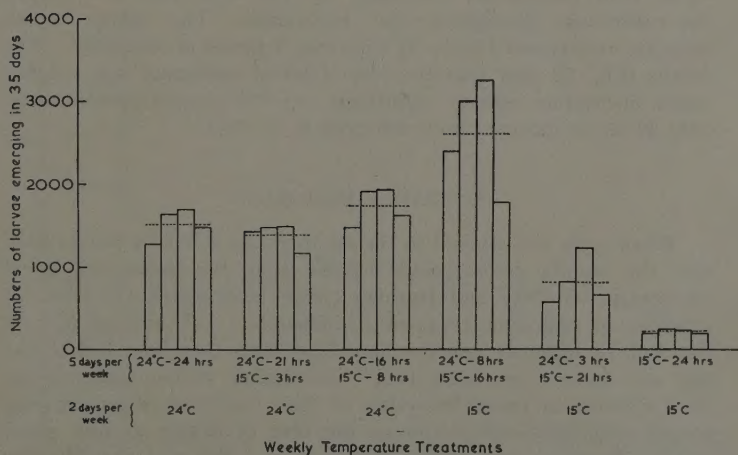


Fig. 2.—Effect of fluctuating temperature on larval emergence. The horizontal dotted lines indicate the mean of four replicates.

were counted. Interpretation of the results (Fig. 3) is difficult since a constant oxygen concentration could not be maintained in the system just described. There was a considerable drop in oxygen concentration by the end of the experiment, but the technique does give a measure of the relationship between available oxygen and emergence. It is clear that the rate of emergence increased as the initial oxygen concentration increased. At initial oxygen concentrations approaching zero, emergence was almost nil.

The effect of pre-treating cysts at low oxygen concentrations on subsequent emergence in beet diffusate was studied in another experiment. Cysts were placed in distilled water containing about 2 mg. of oxygen per litre for various periods of time. After treatment they were placed in beet diffusate and the numbers of larvae that emerged were counted weekly. The results (Fig. 4) suggest that the rate of emergence was decreased by exposure to low oxygen concentrations for quite short periods of time.

Under field conditions the oxygen concentration of the soil water fluctuates (Bayer, 1948). In order to investigate the effect of such conditions on larval emergence, cysts in beet diffusate were subjected to alternating low and high oxygen concentrations. In addition, cysts were maintained constantly at the high and low oxygen concentrations throughout the experiment. The larvae which emerged were counted every $3\frac{1}{2}$ days over a period of ten weeks. The results (Fig. 5) show that the rate of larval emergence was reduced under fluctuating oxygen conditions. At low oxygen concentration only 20 larvae emerged from 500 cysts in 70 days.

SATURATION DEFICIENCY.

When cysts are exposed to the air they lose water by evaporation and the results given below suggest that this influences larval emergence. Godfrey and Hoshino (1953) investigated the effect of exposure of eggs and larvae of *H. radiculicola* (= *H. marioni* (Cornu) Goodey) to different relative humidities and they found that the egg and larval "mortality rate" was higher at lower humidities. It is difficult to assess the value of their results since temperature varied from 20°C.-28°C. and so the rate of drying at any given relative humidity varied with temperature. Mai and von Mechow (1952) investigated the effect on "viability" of storing cysts of *H. rostochiensis* in different humidities for various periods of time.

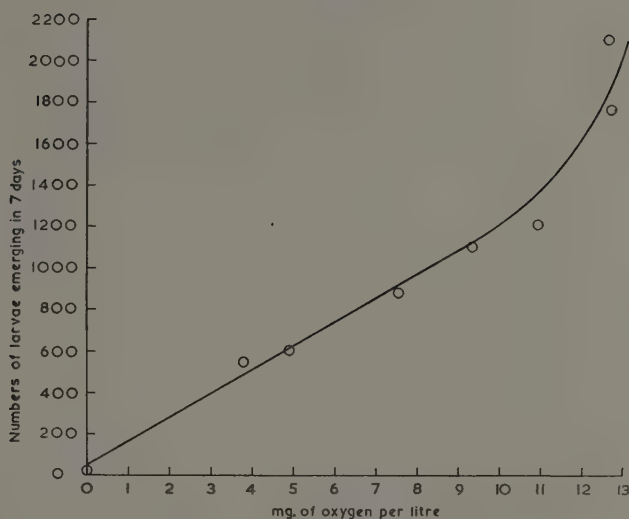


Fig. 3.—Effect of initial oxygen concentration on larval emergence in distilled water at 25°C.

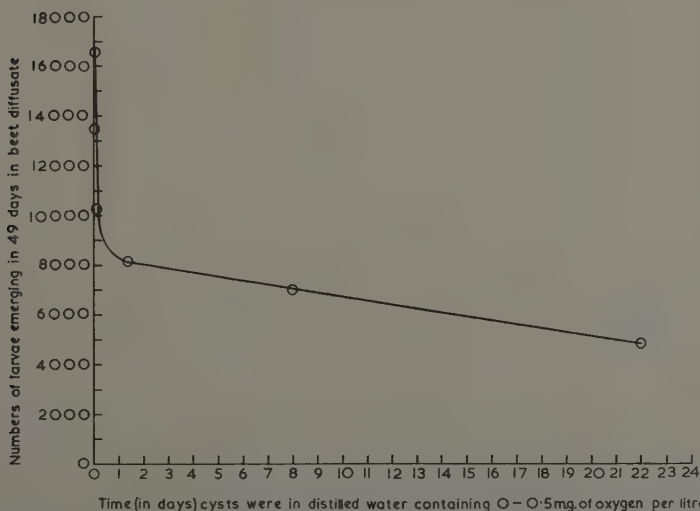


Fig. 4.—Effect of pre-treatment of cysts at a low oxygen concentration for various periods of time, on subsequent larval emergence.

Saturation deficiency measures the drying power of the air and combines the factors of temperature and humidity. An experiment was performed to ascertain the rate of loss of water from cysts in air at different saturation deficiencies, the cysts being pre-soaked for a week to ensure that they were filled with water at the start of the experiment. They were placed on filter paper to remove surplus

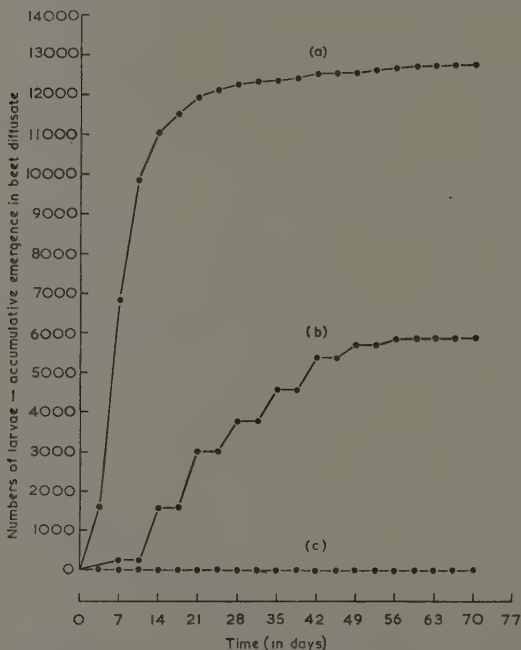


Fig. 5.—Effect of constant and fluctuating oxygen conditions on larval emergence. (a) constant high oxygen concentration, (b) fluctuating high and low oxygen concentrations, (c) constant low oxygen concentration.

moisture and then transferred to small trays suspended over solutions of caustic-potash in air-tight tubes. By varying the concentration of caustic-potash, six different saturation deficiencies were obtained. The cysts were weighed at intervals on a torsion balance and the results are given in Fig. 6. The time to reach constant weight varied inversely as the saturation deficiency, but the relationship is not

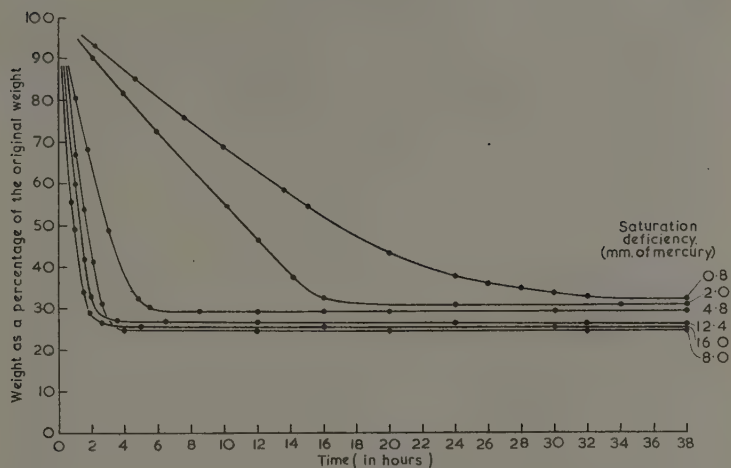


Fig. 6.—Loss of weight of cysts in different saturation deficiencies over a 38-hour period.

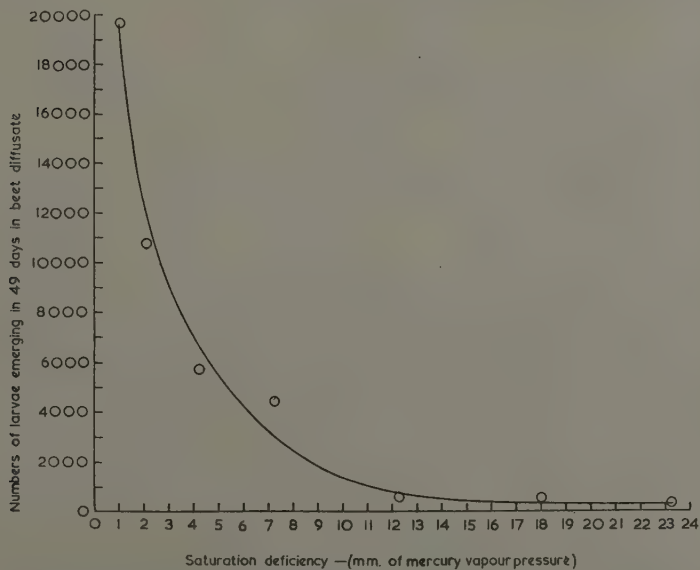


Fig. 7.—Effect of pre-treatment of cysts at different saturation deficiencies for 12 days, on subsequent larval emergence.

linear, the contents of the cysts retaining water more tenaciously as the saturation deficiency increased. In this respect the cyst contents behave as do other colloidal systems.

The effect on larval emergence of pre-treatment of cysts at different saturation deficiencies for a given length of time was also studied. Cysts were subjected to seven different saturation deficiencies for 12 days and then placed in beet diffusate. Weekly counts of larvae were taken and the results are given in Fig. 7. The subsequent rate of larval emergence is greatly reduced by small increases in saturation deficiency, between 1 and 8 mm. of mercury vapour pressure during pre-treatment.

By pre-treating cysts at a high saturation deficiency of 24.9 mm. mercury vapour pressure, the subsequent larval emergence in beet diffusate was decreased, the extent of the decrease depending on time of exposure to the treatment (Fig. 8). It seems likely that the steep part of the curve corresponds to the removal of "free" water from the cyst whilst the relatively flat part corresponds to the removal of water held by the colloidal cyst contents.

TABLE I.

Mean number of larvae emerging from 100 cysts in 28 days after pre-treatment.
The first column corresponds to no pre-treatment.

| Pre-treatment period of exposure (in days) | | 0 | 7 | 14 | 21 | 28 | 35 |
|---|-----|-----|-----|------|------|------|------|
| Saturation deficiency | 9.0 | | 613 | 365 | 850 | 28 | 5 |
| (mm. mercury vapour | — | 785 | | | | | |
| pressure) | 1.1 | | 851 | 1167 | 1186 | 1557 | 1026 |

The result of pre-treating cysts at a high and a low saturation deficiency for different times is shown in Table 1. It is evident that cysts which were exposed to the low saturation deficiency subsequently gave a higher emergence rate in diffusate than those which were not pre-treated, while cysts subjected to a high saturation deficiency tended to have a reduced rate of emergence in diffusate.

SOIL MOISTURE.

Eelworms are essentially hydrophilous and their emergence from the cyst and movements through the soil are influenced by the properties of the soil water. Linford (1941) studied the influence of

soil moisture on the viability of egg masses in *H. marioni*. He considered that many eggs died at soil moisture contents less than the wilting coefficient, whilst most of the eggs remained alive above this level; with increasing moisture content hatching was progressively more rapid.

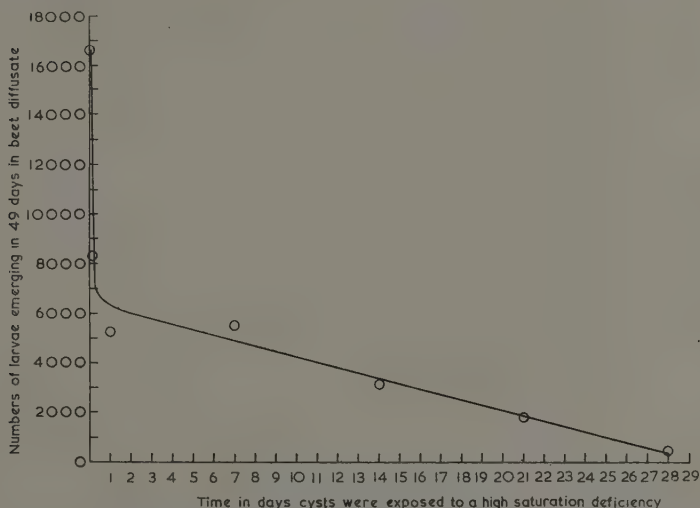


Fig. 8.—Effect of pre-treatment of cysts at a high saturation deficiency of 24.9 mm. mercury vapour pressure for various periods of time on subsequent larval emergence.

The water content of a soil is largely determined by the moisture retaining or suction properties of the soil. The pressure at which such water is held in the soil is always less than that of the atmosphere and is termed pressure-deficiency or suction (Baver, 1948; Russell, 1950). When the moisture content of the soil is reduced, the pressure-deficiency increases and the relationship between the pressure-deficiency and moisture content for a soil is called the moisture characteristic. Pressure-deficiency is expressed as the height in cm. of a water column which the pressure-deficiency would support. In the following experiments the suction-plate method was used to determine the relationship between moisture content and pressure-deficiency. Wallace (1954) showed that when the soil was saturated, a relatively low emergence occurred, probably because of the low

oxygen concentration in the water around the cysts. An increase in emergence occurred when air appeared in the soil pore-spaces. Maximum emergence corresponded approximately to the pressure-deficiency at which the last pore space was emptied of water. At higher pressure-deficiencies there was a decline in the numbers of larvae emerging. It was suggested that a possible explanation of this decline was that hatching of the larvae from the eggs was inhibited by extraction of water from the cysts.

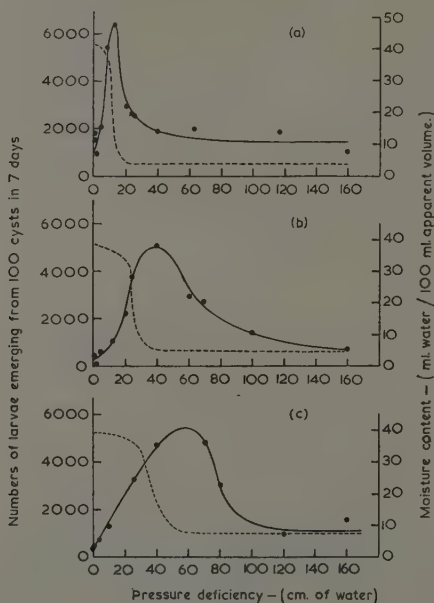


Fig. 9.—Effect of pressure-deficiency on larval emergence in water in three different sand fractions. (a) 200–1800 μ , (b) 60–120 μ , (c) 20–80 μ .

It seems likely therefore, that larval emergence in a soil is related to the moisture characteristic of that soil. To test this hypothesis further, two experiments were carried out to determine the moisture characteristic and larval emergence curves for sands and soils of

different known particle sizes. The method was that of Wallace (1954) and the results obtained are shown in Figs. 9 and 10. It is evident that with increasing particle size the pressure-deficiency necessary for maximum emergence decreased.

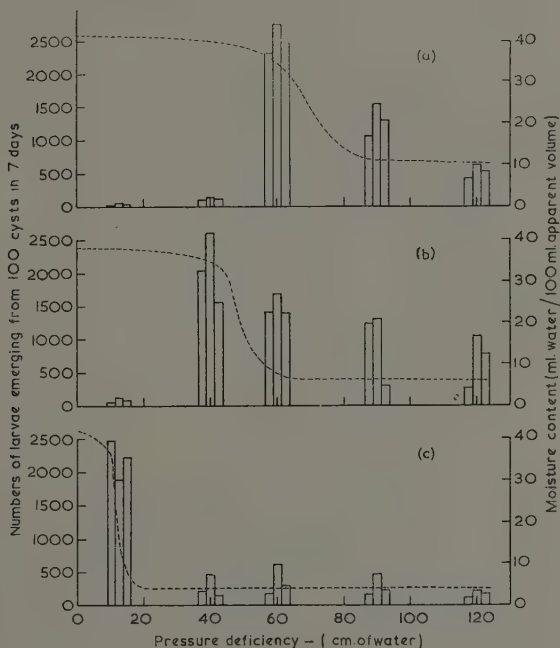


Fig. 10.—Effect of pressure-deficiency on larval emergence in water in three media of different particle sizes. (a) Woburn soil 75–150 μ , (b) Woburn soil 150–250 μ , (c) sand 200–1800 μ .

DISCUSSION.

It is difficult to relate the results of controlled experiments in the laboratory to conditions in the soil, where interdependent physical factors are continually fluctuating. In the laboratory, experiments were designed so that there were as few variables as possible and attempts were made to maintain the other physical conditions at a constant level. The influence of fluctuating conditions was

investigated in two cases only (Figs. 2 and 5). Constant temperatures do not provide optimum conditions for larval emergence and the results suggest that a higher rate of emergence may occur under fluctuating temperatures. The results of another experiment showed that fluctuating oxygen concentrations reduced the emergence rate.

Experiments on the pre-treatment of cysts at low oxygen concentrations and high saturation deficiencies showed that the subsequent rate of larval emergence in diffusate in watch-glasses was reduced. These results emphasise that account must be taken of the previous treatment of cysts when experiments on larval emergence are undertaken.

Larval emergence in watch-glasses is higher in beet diffusate than in tap-water. However, a rate even higher than the diffusate emergence in watch-glasses occurred in the absence of diffusate, in a medium of sand and water only, in sintered-glass funnels, the pressure-deficiency of the water in the sand being adjusted to the optimum level for emergence. The results in terms of total emergence in seven days from five replicates of 100 cysts are set out as follows:—

| <i>Watch-glasses</i> | | <i>Sintered-glass funnels</i> |
|----------------------|-----------------------|-------------------------------|
| <i>tap-water</i> | <i>beet diffusate</i> | <i>tap-water</i> |
| 363 | 1,249 | 10,079 |

The results suggest that oxygen concentration in the watch-glasses was a limiting factor. This has been confirmed by oxygen determinations of diffusate kept in watch-glasses. The oxygen concentration dropped from 10.1 to 6.8 mg. of oxygen per litre in 21 hours, when equilibrium was reached. The use of watch-glasses in experiments may, therefore, influence the amount of available oxygen, especially if micro-organisms are present, and so lead to high variability in the results.

Studies of larval emergence in sintered-glass funnels suggest that in the soil there is a considerable larval emergence from beet eelworm cysts in the absence of active root diffusate from plants, provided the oxygen concentration is at a sufficiently high level.

Larval emergence is influenced by the moisture characteristic of the soil (Figs. 9 and 10). Boyd (1948) states that fewer and smaller cysts of potato-root eelworm are produced on hosts grown in clay than on hosts grown in sand. Kincaid (1946) suggests that soil texture is a factor in movement of larvae of *H. marioni*. Different types of soil

have characteristic physical properties (Baver, 1948) and it seems likely, therefore, that the rate of larval emergence is influenced by the nature of the soil. Rapid emergence in light, well aerated soil might lead to a higher invasion rate of host roots and to more severe crop symptoms than a lower and more protracted emergence in heavier soil at the same population level.

SUMMARY.

Experiments on larval emergence in a series of constant temperatures showed that, of those temperatures tested, 25°C. was the optimum. Results suggest that constant temperatures do not provide optimum conditions for larval emergence and that a higher rate of emergence may occur under fluctuating temperatures. The rate of larval emergence in beet diffusate increased as the initial oxygen concentration increased. Pre-treatment of cysts at low oxygen concentrations reduced the subsequent emergence in diffusate. Fluctuating oxygen concentrations also reduced emergence. The rate of loss of water from cysts in air at different saturation deficiencies was determined and the results suggest that the cyst contents behave like other colloidal systems. By exposing cysts to different saturation deficiencies for a given length of time, the subsequent rate of larval emergence in beet diffusate was reduced. A similar result was obtained by pre-treating cysts at a high saturation deficiency for various intervals of time. Larval emergence was found to be dependent on the moisture characteristic of the soil. With increasing particle size, the pressure deficiency necessary for maximum emergence decreased. The bearing which these results have upon emergence of larvae in laboratory experiments and in the soil are briefly discussed.

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Observations on Some Helminth Parasites from Ducks in Southern England

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Apart from records of the occurrence of many species of helminth parasites in British poultry and game birds by Nicoll (1923), Baylis (1928, 1939), Lewis (1930), Morgan (1932), Foggie (1933), Davies (1938), Morgan and Wilson (1938, 1939), Clapham (1935, 1936, 1937, 1938a, 1938b, 1940), Taylor (1938), Watkins (1947) and Owen (1951), little study of the parasitic infections of birds in Britain has been carried out. In England, the Poultry Technical Committee (1938) regarded parasitic infections of the domestic fowl as one of the three main causes of mortality in these birds and emphasized the fact that more research was required to assess the effect of such infestations on the general condition of the birds, their growth and productivity.

Between 1930 and 1940, Hoffman and Stover (1942) in America carried out an intensive survey into the causes of death among fowls and recorded the results of autopsies of 30,000 birds. They attributed 6 per cent. of the total deaths to intestinal nematodes, 1.5 per cent. to cestodes and 1 per cent. to gizzard worms.

As far as the pathogenesis of most of the helminth parasites of domesticated birds is concerned, little is known. Hence accurate diagnosis of the real cause of death, or of the factors associated in the production of disease is always attended with difficulty. Taylor (1938) mentioned that of the 150–200 helminth species so far met with in domesticated birds, only two could be considered with certainty as the principal cause of mortality. These two are *Syngamus trachea*, the gapeworm of fowls, and *Amidostomum anseris*, the gizzard-worm of geese. The significance of this statement is a realised fact to research workers in this field, since infestations with helminth parasites in small numbers may frequently be seen in a large percentage of birds where no lesions are apparent. Nevertheless, when a large number of parasites, other than the two previously mentioned by Taylor (1938), are met with, such infestations may be regarded as harmful, though no characteristic lesions are recognized as a guide for diagnosis.

The interest in the present work arose as a result of the investigation of Rollinson, Soliman and Mann (1950), who recorded the finding of leeches of the species *Theromyzon tessulatum* (= *Protolepsis tessellata*) in the nasal cavities of young ducklings that died on a farm near Wantage, Berkshire, during the autumn of 1949. The cause of death in these ducklings has not been definitely established. Pathological, bacteriological and parasitological examinations gave no significant results. Subsequently specimens of *Theromyzon tessulatum* were collected from the millpond on which the dead ducklings had lived, and experimental infestation of healthy young ducks was carried out. However, no evidence of anaemia, which might have been induced by the leeches sucking blood, could be demonstrated. The owner was advised to keep young ducklings away from the millpond until they were over three months old. Dr. Mann of the Zoological Department, University of Reading, who identified these leeches, became interested in the bionomics and distribution of *T. tessulatum* and began to collect specimens of this species. Among those he subsequently collected in the vicinity of Reading, there was a specimen of the leech *Erpobdella octoculata*, in which a large number of cysticeroids was observed in the mesenchyme (See Fig. 1). Careful examination of the number, shape and size of the hooks in these cysticeroids showed them to be referable to *Hymenolepis parvula* Kowalevski, 1904 (See Fig. 2). During the two successive years, 1950 and 1951, contact was kept with the farm, and no further losses were reported among the ducks. Towards the end of August, 1952, however, a visit was made to the millpond as the keeper there had observed some young ducklings swimming on the pond. He accounted for the presence of these by the fact that some Khaki Campbell ducks had laid their eggs in a nearby shrubbery and hatched them towards the end of June, 1952. Their exact number was not known, but the brood consisted of about eight birds. After about three weeks this number began to diminish. Accordingly a search was made, and the only bird that could be found was one young duckling, about one and half months old. It was seen feebly swimming about under the bushes around the edge of the pond.

Having in mind the finding of *Hymenolepis parvula* cysticeroids in the mesenchyme of Dr. Mann's specimen of *Erpobdella octoculata* in 1949, it was thought advisable to search for similar specimens that might be present. A number of leeches were thus collected from the pond and taken to the Veterinary Investigation Laboratory at Reading for examination. Two species of leeches were identified,

namely, *Erpobdella octoculata* and *Theromyzon tessulatum*. From the first species of leech about twelve cysts were dissected. These cysts were all of the same type and each contained a metacercaria of a strigeid trematode. A number of *Erpobdella octoculata* containing these cysts were then stained with acid alum carmine and examined (See Fig. 8). The cysts were observed scattered in the mesenchyme of the leech and measured 250 to 308 microns in length by 185 microns in breadth. The metacercariae within these cysts measured 208 to 238 microns by 146 microns and each was provided with an oral and a ventral sucker of circular outline, each measuring about 35 microns in diameter. Mr. S. Prudhoe of the British Museum (Natural History) examined a sample of these cysts, and he reported the metacercaria as probably that of *Cotylurus cornutus* (Rud., 1809), a species frequently found as adults in the intestines of ducks. At that stage it was decided to make a study of the parasites that might be found in ducks living on the farm.

The object of this paper, apart from recording certain helminth parasites met with in ducks in England, some of which are new records for Britain, is to assess the extent of infestation in birds examined and to describe lesions associated with the infections, as well as to account for the conditions under which the infections were acquired.

MATERIAL AND METHODS.

The data here presented were obtained from the examination of six Muscovy and twelve Khaki Campbell ducks during the summer of 1952. All of the eighteen ducks were alive when collected and, with the exception of the first one examined, which was a young duckling surviving from the brood that hatched in the shrubbery around the millpond, all were in an active and healthy condition. Although the number examined is small, the findings have their significance.

In carrying out this study the respiratory and digestive tracts were examined, and the mesenteric veins were carefully, but unsuccessfully, searched for *Bilharziella*. The digestive tract was examined in three separate region, viz :—

1. Gullet, proventriculus and gizzard. 2. Small intestines (duodenum, jejunum and ileum). 3. Large intestines.

Special attention was given to the duodenal region for *Hymenolepis parvula*, the cysticeroids of which occurred in mesenchyme of

Erypoddella octoculata and are mentioned above. The parasites recovered were then identified and counted; the sex of the nematodes was also noted.

The Helminth Parasites recovered from Khaki Campbell and Muscovy ducks.

The first bird examined was the young Khaki Campbell duckling that was observed towards the end of August, 1952, a survivor of the brood hatched in the shrubbery. It was killed, and a post-mortem was carried out on the 10th September, 1952. The systematic examination previously mentioned under methods was followed and the following parasites were recovered.

TREMATODES :

Echinoparyphium recurvatum (Linstow, 1873), small intestines ;
over 2,000 immature specimens.

Hypoderaeum conoideum (Bloch, 1872), small intestines ;
about 100 immature specimens.

Notocotylus attenuatus (Rud., 1809), large intestines ;
about 1,500 specimens, most of which were immature.

Cotylurus cornutus (Rud., 1809), small intestines ;
52 immature specimens.

CESTODES :

About 750 specimens were collected and comprise the following species :—

Hymenolepis anatina (Krabbe, 1869), small intestines.

Hymenolepis collaris (Batsch, 1786), small intestines.

Hymenolepis coronula (Dujardin, 1845), small intestines.

Most of this material appeared to be referable to *H. coronula*, which has been recorded from the domestic duck in Wales by Owen (1951) and from the Golden-eye duck in London by Baylis (1939).

NEMATODES :

Forty specimens have been collected and comprise the following two species :—

Tetrameres fissispina (Diesing, 1861), proventriculus ; eight females embedded in the glandular tissue and five males free in the proventriculus.

Trichostrongylus tenuis (Mehlis, 1846), small intestines (ileum) ; five females and five males.

ACANTHOCEPHALA :

Filicollis anatis (Schrunk, 1788), small intestines; sixty specimens in various stages of development.

Careful search of the duodenum failed to reveal the existence of *H. parvula*. It was thus thought advisable to examine a number of the healthy adult birds. Table I summarises the parasitological findings resulting from post-mortem examination of eleven adult Khaki Campbell ducks.

TABLE I.

The helminth parasites recovered from eleven Khaki Campbell ducks over one year old.

| Species of Parasite | No. of ducks infested | Total no. of parasites recovered | Range of nos. in infested ducks | Mean no. per infested duck |
|-----------------------------------|-----------------------------|---|--|-------------------------------------|
| <i>Echinoparyphium recurvatum</i> | .. 3 | 71 | 17-29 | 23.6 |
| <i>Hypoderaeum conoideum</i> | 3 | 17 | 2-10 | 5.4 |
| <i>Notocotylus attenuatus</i> | 5 | 163 | 4-17 | 32.6 |
| <i>Hymenolepis anatina</i> | 4 | 36 | 3-11 | 9.0 |
| <i>Hymenolepis coronula</i> | 11 | 65 | 4-19 | 5.9 |
| <i>Hymenolepis collaris</i> | 10 | 60 | 3-11 | 6.0 |
| <i>Hymenolepis gracilis</i> | 2 | 23 | 5-18 | 11.5 |
| <i>Trichostrongylus tenuis</i> | 5 | 17 | 1-6 | 3.4 |
| <i>Heterakis gallinae</i> | 7 | 28 | 2-11 | 4.0 |
| <i>Filicollis anatis</i> | 2 | 15 | 4-11 | 7.5 |

Table II summarises the parasitological results obtained from post-mortem examination of the six Muscovy ducks.

TABLE II.

The helminth parasites recovered from six Muscovy ducks over one year old.

| Species of Parasite | No. of ducks infested | Total no. of parasites recovered | Range of nos. in infested ducks | Mean no. per infested duck |
|-----------------------------------|-----------------------------|---|--|-------------------------------------|
| <i>Echinoparyphium recurvatum</i> | 2 | 21 | 2-17 | 10.5 |
| <i>Notocotylus attenuatus</i> | 3 | 121 | 5-57 | 40.3 |
| <i>Hymenolepis anatina</i> | 2 | 29 | 5-24 | 14.5 |
| <i>Hymenolepis coronula</i> | 6 | 197 | 15-31 | 32.8 |
| <i>Hymenolepis collaris</i> | 3 | 37 | 9-13 | 12.3 |
| <i>Hymenolepis gracilis</i> | 4 | 57 | 5-21 | 14.2 |
| <i>Hymenolepis abortiva</i> | 2 | 36 | 13-23 | 18.0 |
| <i>Trichostrongylus tenuis</i> | 4 | 37 | 5-15 | 9.3 |
| <i>Filicollis anatis</i> | 6 | 118 | 9-27 | 19.6 |

DISCUSSION.

From the foregoing results it may be stated that four species of Trematodes, five species of Cestodes, three species of Nematodes and one species of Acanthocephala have been encountered. The occurrence of some of these parasites in various wild birds in England has been recorded by other workers, but not hitherto from ducks, and certain of the species mentioned above are here recorded for the first time. In accordance with this statement and the pathogenesis of the species recorded, as observed from post-mortem examinations, the following observations may be mentioned.

TREMATODES :

Echinoparyphium recurvatum (Linstow, 1873) and *Hypoderaeum conoideum* (Bloch, 1809), have been recorded from the domestic duck in Britain by Owen (1951). Nicoll (1923) listed *Notocotylus attenuatus* (Rud., 1809) as a possible parasite of the domestic duck in Britain, while Foggie (1933) found this species in ducks believed to have been reared in the South of England. The latter author also recorded *Cotylurus cornutus* (Rud., 1809), under the name of *Strigea tarda*, in ducks from the same source in 1933. No visible pathological changes have been observed in any of the infested ducks, not even in the young duckling, which was very heavily parasitized with these four species. Presumably, such a heavy infestation is apt to interfere with the normal function of the small intestines, where most of the parasites were located. The possibility of the effect of toxins produced by these parasites on their host should also be considered.

CESTODES :

Hymenolepis coronula (Dujardin, 1845) and *Hymenolepis gracilis* (Zeder, 1803) have both been recorded from the domestic duck in Britain by Owen (1951).

Hymenolepis collaris (Batsch, 1786) does not appear to have been recorded from the domestic duck in Britain, though Baylis (1929 and 1939) has recorded specimens, previously referred to this species, from the Mallard in Hertfordshire and Norfolk.

Hymenolepis anatina (Krabbe, 1869) does not appear to have been hitherto recorded from any host in Britain.

Hymenolepis abortiva (Linstow, 1904) also does not appear to have been recorded from Britain. Specimens of this cestode obtained during the present survey correspond to the description given by Meggitt (1927).

No visible pathological changes were observed in any of the ducks parasitized with these species. Nothing more could be added to what has already been mentioned in connection with the Trematode infection, other than that these species may have greatly contributed to the unmistakable anaemia observed in the young duckling.

NEMATODES :

With the exception of *Heterakis gallinae*, the presence of the other two nematodes seems to have a special significance. *Tetrameres fissispina* (Diesing, 1861) was found only infesting the proventriculus of the young duckling. According to Lang (1938), this parasite may cause serious losses among ducks. Owen (1951) has given a history of its occurrence in Britain, recording it from three ducks and some wild birds. Monnig (1947) and Watkins (1947) have alluded to the harmful effect of infection with this nematode. The proventriculus of the duckling was slightly inflamed and the female parasites were readily observed embedded in the glandular tissue (See Fig. 4). When these were dissected out, measured and examined, they were found to be fully mature, reaching full size, although the host was under two months old.

Trichostrongylus tenuis (Mehlis, in Creplin, 1846), though recorded from fowl, grouse, partridge, domestic goose, turkey and wild anatine birds by Clapham (1938b), Morgan and Wilson (1938) and Owen (1951), does not appear to have been recorded from the domestic duck in Britain. In the present work this species has been met with in ten ducks out of eighteen, that is in about 55 per cent. of the ducks examined. In the duckling it was found in the region of the distal portion of the small intestine (ileum), while in the other nine adult ducks it was recovered from the caeca. The number of parasites recovered ranged from 1 to 15 with an average of 6.4 per infested bird. The sexes of the worms were nearly equal in number.

ACANTHOCEPHALA :

Filicollis anatis (Schränk, 1788). Though this parasite was listed from mallard and scaup duck by Baylis (1928), it has not been recorded previously from the domestic duck in Britain. Nine ducks out of eighteen (50 per cent.) were infested, and the infestation was rather heavy in the duckling and two of the Muscovy ducks. In these three ducks the proboscis of some female parasites was observed just under the transparent peritoneum covering the intestines (See Fig. 5), and the parasites were seen distributed through the last

two-thirds of the small intestines. It was interesting to find the infestation with this parasite among the Muscovy ducks amounted to almost 100 per cent., while it was only 25 per cent. among the Khaki Campbells. This might be accounted for by the fact that the water-louse, *Asellus aquaticus*, which acts as an intermediate host for this parasite, was usually found in the shallow water near the bank of the pond. The Muscovy ducks were usually seen on the bank or swimming about in the shallow water, while the Khaki Campbells were observed mostly in the middle of the pond. The first thus had more facility for feeding on the water-lice than the second kind of ducks. Hence the difference in the percentage of infection in the two groups.

Conditions under which the infections are assumed to have been acquired.

The ducks had access to a large millpond of about 150 yards long by 100 yards wide, narrowing to 30 yards, with only small areas of bank accessible, owing to the presence of shrubbery. This pond was fed by a stream leading from several other ponds, and was held to a mill race level. The pond was frequented by numerous dabchicks and occasionally wild birds and ducks would alight on it. The possibility of wild birds bringing the infections of the newly recorded parasites to England is obvious. The invertebrate fauna of the pond included most of the intermediate hosts needed in the life-cycle of the parasites encountered. Different kinds of molluscs were in the pond, mainly *Limnaea stagnalis*, *L. pereger* and *Helicella* species; representatives of Isopoda, mainly the water-louse, *Asellus aquaticus*, and water fleas, *Daphnia pulex*. Two species of leeches were identified from this pond, namely, *Erpobdella octoculata* and *Theromyzon tessulatum*.

Although the investigation of the life cycles of some of the parasites recorded was rather out of the scope of the present work, an attempt was made in this direction. A large number of water fleas (*Daphnia pulex*), water lice (*Asellus aquaticus*) and other freshwater Crustacea collected from the pond was carefully examined. No larval stage of *Tetrameres fissispina* was observed in any of the material collected. This might be explained by the fact that this last parasite was found only in the duckling, and a more intensive search might have been needed to find its larval stage. However, in the water-lice (*Asellus aquaticus*), the larval stage of *Filicollis anatis* was found in 30 out of 120 specimens examined, or in 25 per cent. of the material. The trematode cysts observed in the mesenchyme of

the leech *Erpobdella octoculata*, mentioned earlier, gave the impression that they contained the metacercariae of a strigeid trematode, probably *Cotylurus cornutus* (Rud., 1809). Leeches of this species were numerous in the pond and commonly infested with these cysts, but feeding experiments must be carried out on the ducks before the identity of this parasite can be ascertained beyond doubt.

SUMMARY.

1. Thirteen different species of helminth parasites were encountered in eighteen ducks (six Muscovy and twelve Khaki Campbells) on a farm in Berkshire. Of these parasites, four were trematodes, five cestodes, three nematodes and one Acanthocephala.

Hymenolepis collaris, *Trichostrongylus tenuis* and *Filicollis anatis* are recorded from the domestic duck in Britain for the first time. *Hymenolepis anatina* and *Hymenolepis abortiva* are recorded for the first time in England.

2. The finding of cysticeroids of *Hymenolepis parvula* in the mesenchyme of a leech (*Erpobdella octoculata*) is here recorded.

3. The probability that the leech (*Erpobdella octoculata*) acts as the second intermediate host for *Cotylurus cornutus* is discussed.

4. The conditions under which the helminth infections of the ducks have been acquired were investigated.

ACKNOWLEDGMENTS.

The writer wishes to express his gratitude to Dr. N. S. Barron, V.I.O., Reading, for facilities given at his laboratory, and to Mr. S. Prudhoe, British Museum (Natural History), for his willing help in the identification of some of the species recorded and for making available facilities for tracing literature needed. Thanks are also due to Dr. I. Abou Bakr, Director of Vet. Research Inst., Egypt, for reading this manuscript, and to Dr. K. H. Mann, University of Reading, for the photographs No. 1 and 2, and to Mr. Hassan Ismail, Photo Section, Agriculture Museum, Cairo, for the other photographs.

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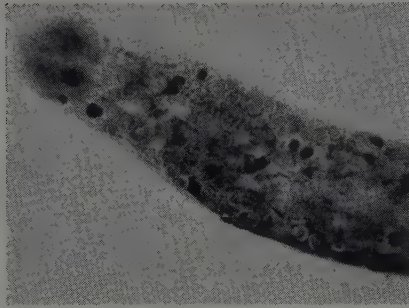


Fig. 1.—Posterior half of leech, *Erpobdella octoculata*, showing cysticercoids of *Hymenolepis parvula*. X 10.

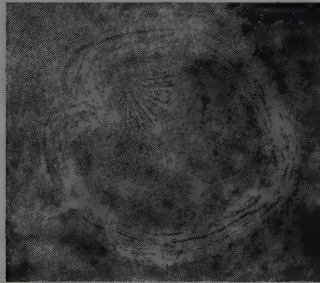


Fig. 2.—Cysticercoid of *Hymenolepis parvula* in mesenchyme of leech, *Erpobdella octoculata*. X 150.

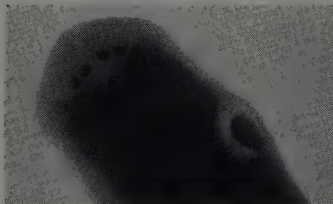


Fig. 3.—Anterior part of leech, *Erpobdella octoculata*, showing encysted metacercaria of a strigeid trematode. X 17.

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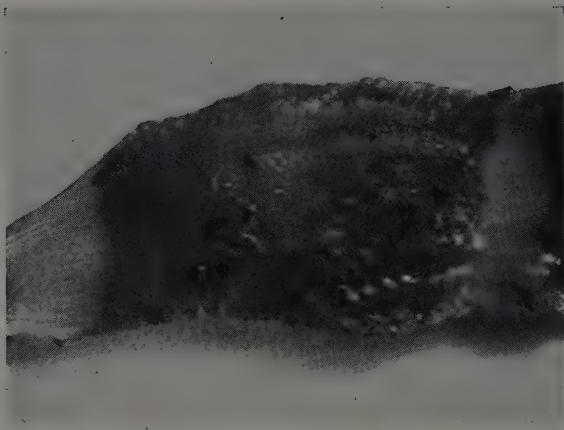


Fig. 4.—Proventriculus of duckling, opened up to show *Tetrameres fissispina* (females) embedded in glandular tissue. X 3.



Fig. 5.—Small intestine of duckling showing probosces of *Filicollis anatis* (females) just under peritoneum, having pierced the mucous and muscular layers. X 4.

Some Observations on the Transmission of Bacteria by Infective Larvae of *Nippostrongylus brasiliensis

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It is well known that the first two larval stages in the life cycle of nematodes belonging to the superfamily Strongloidea, have a free-living existence. During this time, the larva which hatches from the egg feeds actively, undergoes two moults and grows considerably before reaching the infective stage, when it is ready to invade a definitive host. Under natural conditions this external development takes place in the faeces, which have been deposited by the infected host on ground likely to be contaminated with various bacteria.

In the laboratory McCoy (1929) succeeded in hatching eggs of *Ancylostoma caninum* in agar cultures of 22 different kinds of bacteria and the larvae developed to the infective stage. Lapage (1939) has pointed out that the infective larvae reared on cultures of *B. coli* may contain in their intestines, bacteria picked up from these cultures before they have become unsheathed. Kawanishi (1929) recovered various bacteria from the surface of *Ancylostoma* larvae. Shope (1941) demonstrated that the pig lung-worms *Metastrongylus elongatus* and *Choerostrongylus pudendotectus* were capable of harbouring swine influenza virus and of transmitting it.

If, therefore, pathogenic bacteria are present in faeces in which infective larvae develop, these bacteria might remain alive long enough inside or on the surface of the larvae, to be inoculated directly into the body tissue of the host.

* Part of a thesis approved by the University of London for the award of the Ph.D. degree.

I. *The identity of the micro-organisms inside and/or adherent to the surface of the infective larvae of N. brasiliensis from normal cultures.*

MATERIAL AND METHODS.

The infective stage larvae, five days old, used for this study were hatched on filter paper, using activated alumina as an absorbent, according to the technique described by Barakat (1951). A piece of the edge of the filter paper, containing larvae, was cut and held by a pair of forceps in such a way as to leave the larvae at the edge of the filter paper free. The edge of the paper bearing the larvae was exposed to the surface of a blood agar plate and only the anterior part of the larvae which protrude from the sheath was allowed to touch the medium. When the larvae were in contact with the surface of the agar, they migrated on to the medium, which was afterwards incubated at 37°C. The larvae were noticed to move actively on the surface and into the agar. Another piece of the filter paper, cut nearer to the edge, was inoculated into a cooked meat medium. All the media were incubated at 37°C. for 24 hours.

RESULTS.

The micro-organisms recovered were kindly identified by Dr. McCloy of the Bacteriology Department, London School of Hygiene and Tropical Medicine. The organisms were:—

- (1) *B. coli* (5 strains).
- (2) Haemolytic streptococcus (2 strains).
- (3) *Streptococcus faecalis*.
- (4) *Cl. tertian* (non-pathogenic).
- (5) *Cl. oedematiens*.
- (6) One of the clostridium group (not identified).

Some of the above-mentioned organisms were also demonstrated in direct smears and cultures which were sown from the faeces of rats infected with *N. brasiliensis*.

CONCLUSION.

This finding suggests that the faecal bacteria recovered from the surface of the larvae may have been utilized as food by the larvae or they may have been carried mechanically from direct contact with the faeces.

II. *The application of pathogenic micro-organisms and infective larvae to the intact abdominal skin and recovery of the former from the subcutaneous tissue.*

MATERIAL AND METHODS.

Albino rats and mice, of ages varying between four and six weeks were used. All animals had been proved by repeated examinations of their faeces to be free from *N.brasiliensis* infection. In each experiment three groups of animals were used. In group "1" infective larvae were applied to the skin, in group "2" bacterial emulsion was only applied to the skin and in group "3" bacteria plus larvae were applied.

The bacteria used in these experiments were *Staphylococcus aureus* and *Streptococcus pyogenes* and consisted of 48 hours nutrient broth cultures and cultures sown on blood agar incubated at 37°C. which were mixed together.

The infective stage larvae of *N. brasiliensis* were cultured on filter paper, using activated alumina as an absorbant. The infective stage larvae, as recovered from the edge of the filter paper, were applied to the intact skin of the abdomen. They were not treated with any disinfectant.

The infectivity of the larvae was tested by exposing two rats to infection with the same culture of the larvae as used in each of the experiments, and in each case the larvae proved to be infective, as eggs of the parasite were recovered when faeces were examined a week after exposure.

Animals were anaesthetised with ether and secured, abdomen upwards. The hair was clipped from a square in the middle of the abdomen of each animal and great care was taken not to injure the skin. The site of exposure was examined under a hand lens (XI2) to make certain that the skin was quite intact and it was then damped with sterile filtered water. The bacterial culture grown on the blood agar was transferred to that in the serum broth and then to the prepared site in the animals of group "3". 0.3 ml. of the emulsion of the selected organism, and 500 infective larvae, were applied. The same dose of emulsion only was applied to the site in animals of group "2." To group "1" only 500 infective larvae were applied and 0.3 ml. of sterile filtered water was added. A quarter of an hour after exposure, 0.3 ml. of the emulsion was added to the selected site in each animal of groups "2" and "3" and 0.3 ml. of sterile filtered water

to the animals in group "1." To insure the penetration of a maximum number of parasites into the subcutaneous tissues the animals were kept secured in position for 2 hours, after which the site of exposure and the area around it were disinfected with 5 per cent. tincture of iodine. The animals were then killed by chloroformation and the abdominal skin was aseptically dissected exposing the under surface of the skin at the site of infection. All procedures were carried out as aseptically as possible. A platinum loop was used to make smears from the subcutaneous tissues under the site of infection in groups "2" and "3," and these were inoculated into nutrient broth media

TABLE I.

| Rat No. | Micro-organisms recovered from the subcutaneous tissues | | |
|---------|---|------------------|--------------------|
| | Group "1" | Group "2" | Group "3" |
| 1 | | | Staph aureus |
| 2 | | | " " |
| 3 | In all animals | No bacteria | " " |
| 4 | Gram-negative | were recovered | " " |
| 5 | bacilli + | from these rats. | " " |
| 6 | Streptococcus | | " " |
| 7 | organisms. | | " " + Gram—bacilli |
| 8 | | | " " |
| 9 | | | " " |
| 10 | | | " " |
| 11 | | | " " |
| 12 | | | " " |
| 13 | | | " " |
| 14 | | | " " |
| 15 | | | " " |
| 16 | | | " " + Gram—bacilli |
| 17 | | | " " |
| 18 | | | " " |
| 19 | | | " " |
| 20 | | | Negative |

which was incubated at 37°C. for 24 hours. Subcultures were made from these broth cultures on serum and blood agar plates. Morphology of the colonies of bacteria and smears on slides were examined to note whether the bacteria used in the experiment had been conveyed by the larvae into the subcutaneous tissues.

Experiment No. 1. (Staphylococcus aureus).

Group "1" Five rats (6 weeks old) were exposed to larvae.

Group "2" Five rats (6 weeks old) were exposed to bacteria.

Group "3" Five rats (6 weeks old) were exposed to bacteria and larvae.

This experiment was repeated three times. The results of all the

experiments showed that no bacteria were recovered from the subcutaneous tissues of the rats in group "2" which were exposed to bacteria only. In the 20 rats of group "3" which were exposed to bacteria and infective larvae, the micro-organisms (*Staph. aureus*) were recovered from the subcutaneous tissues in 19 out of the 20 rats. In a few of these cases other bacteria (Table I) were also recovered. A gram-negative bacillus and a streptococcus were recovered in all animals of group "1".

Experiment No. 2. (Streptococcus pyogenes).

The experiment using *Str. pyogenes* was carried out on the same lines as the first one. Fifteen mice were used and this experiment was not repeated. The results (Table II) obtained showed that no bacteria were recovered from the mice in group "2" while in group "3" *Str. pyogenes* was recovered from each animal. A Gram-negative bacillus and a streptococcus were recovered from all mice in group "1."

TABLE II.

| Mouse No. | Micro-organisms recovered from the subcutaneous tissues | | |
|-----------|---|-----------|----------------------|
| | Group "1" | Group "2" | Group "3" |
| 1 | A Gram-negative bacillus | Negative | <i>Str. pyogenes</i> |
| 2 | A Gram-negative bacillus | " | " " |
| 3 | A Gram-negative bacillus+ <i>Str.</i> | " | " " |
| 4 | A Gram-negative bacillus+ <i>Str.</i> | " | " " |
| 5 | A Gram-negative bacillus+ <i>Str.</i> | " | " " |

CONCLUSION.

From the above-mentioned experiments it seems reasonable to conclude that the larvae during penetration of the skin introduced the pathogenic bacteria which were recovered from the subcutaneous tissues after the application of the bacteria and infective stage larvae to the intact abdominal skin. The fact that bacteria other than those used in the experiment (experiment I, group "3") were recovered suggests that these bacteria were adherent to the cuticle of the parasite and were either of faecal origin or were present on the skin. The animals which were exposed only to the parasites (group "1") have proved to favour the penetration of micro-organisms into the subcutaneous tissues.

ACKNOWLEDGMENT.

The writer would like to record his gratitude to Professor J. J. C. Buckley and to Dr. P. L. LeRoux, for their valuable guidance, aid and criticism during the preparation of this work. Thanks are also due to Dr. E. W. McCloy, of the Bacteriology Department, London School of Hygiene and Tropical Medicine, for the identification of the bacteria mentioned in this work.

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Observations on Skin Penetration by the Infective Larvae of *Nippostrongylus brasiliensis

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Taliaferro and Sarles (1939) who studied the cellular reaction in the skin, lung and intestine of normal and immune rats after infection with *N. muris*, stated that "larvae were found penetrating the skin from a half hour through two hours after they had been placed on the skin. They seemed to penetrate directly. . ." Yokogawa (1922) observed that this parasite when placed on the skin of rats, penetrated into the tissues very quickly. He did not specify any time for their entrance.

While studying the rôle of tissue-invading helminths in bacterial infections, the writer (1955) found that it was of importance to ascertain the time taken by infective larvae of *N. brasiliensis* to penetrate the skin of their host and for this purpose carried out the following experiments.

DURATION OF SKIN PENETRATION.

Eight mice, three weeks old, which had been proved by repeated examinations of their faeces to be free of the parasite, were secured abdomen upwards by tying gauze round the legs and pinning this to a board. An area in the middle of the abdomen was clipped with scissors, care being taken not to injure the skin. The site was damped with water and 200 larvae were applied to the clipped area of each mouse. The larvae were left for varying lengths of time on each mouse; 5, 10, 15, 20, 30 minutes, 1, 2 and 3 hours respectively. At

* Part of a thesis approved by the University of London for the award of the Ph.D. degree.

the end of each of these periods the site of infection and the surrounding area on each mouse was wiped with 10 per cent. formalin solution, absolute alcohol and then with a weak tincture of iodine (5 per cent.) to ensure that all larvae on the skin were killed. After disinfection each mouse was kept separately in a jar marked with the date and the time of exposure to infection. Forty-eight hours after exposure to infection all the mice were killed. The lymph glands draining the site of exposure and the lungs were then examined for the presence of larvae and the results (see also Table I) were as follows:—

(1) In the mouse exposed for 5 minutes dead larvae were found in the lymphatic glands of the axilla. One of these is shown in Fig. 1. The lung was not infected.

(2) In the mouse exposed for 10 minutes a few larvae were recovered from the lung and none from the lymphatic glands.

(3) In the mouse exposed for 15 minutes no larvae were recovered from the lymphatic glands or the lungs.

(4) In the mouse exposed for 20 minutes dead larvae were recovered from the lymphatic glands and none from the lungs.

(5) In all the mice exposed to the infection for 30 minutes, one hour, two hours, and three hours respectively, larvae were recovered from the lungs and none from the lymphatic glands.

TABLE I.

| Duration of exposure | Result of the examination for the presence of larvae in | |
|----------------------|---|----------|
| | Lymph gland | lung |
| 5 minutes | dead larvae | negative |
| 10 minutes | negative | positive |
| 15 minutes | negative | negative |
| 20 minutes | dead larvae | negative |
| 30 minutes | negative | positive |
| One hour | negative | positive |
| Two hours | negative | positive |
| Three hours | negative | positive |

These results indicate that some of the larvae may penetrate the skin within five minutes. The fact that they were recovered dead in the lymphatic glands may be due to their having been in contact with the applied disinfectants, which caused them to die after penetration.

This experiment was repeated on 15 mice (three weeks old) divided into three groups. The larvae were left on the skin for half an hour, one hour and two hours respectively and in all the animals larvae were recovered from the lungs 48 hours after exposure to infection.

These findings indicate that half an hour or more was sufficient for a number of larvae to penetrate the skin and reach the lungs.

Skin penetration behaviour.

To observe the mode of entry of infective larvae in the early stages of penetration, prior to their disappearance into the skin, a binocular microscope was focussed on the damped abdominal skin of very young mice and rats (one day to one week old). Infective larvae were placed on the area under observation. The fact that the animals were very young and the abdominal skin, in some, was free from hair and had a pale background colour, enabled one to watch easily the behaviour of the parasite prior to, and during penetration of the skin.

The mode of entry of the infective larvae was also studied by the exposure of young mice and rats at ages varying between a few days up to three months and by subsequent skin sections. The animals were killed quarter, half, one, two, three, and six hours after exposure and sections were made of skin taken from the site of exposure. The skin, which was obtained from the ventral surface of the abdomen or the dorsal surface of the back, consisted either of the entire abdominal wall or was cut away from the muscle. It was stretched and pinned out with needles on hollow rectangles of cork before fixation to facilitate sectioning and was fixed either in absolute alcohol or in 10 per cent. formal saline solution. The stains used were haematoxylin and eosin or Giemsa's stain.

When the larvae were applied to the damp skin they were seen to crawl along and to attach themselves to the skin within a few minutes of exposure. It was noticed that the first selected site did not always prove entirely satisfactory to the larvae and they sometimes moved to several spots before finally selecting the site of entry. Some larvae were observed to position themselves with their tails on the skin and the rest of the body more or less perpendicular to the surface of the skin, Figs. 2 and 1a. They remained in that position for sometime after which they bent over in a semi-circle and forced the head end into the *stratum corneum*, Fig. 1c. Other larvae were noticed to be parallel to the surface of the skin while the head of the

parasite forced an entry into the *stratum corneum*, Fig. 1b. Still others attached themselves to hairs and forced an entry by way of the hair follicles (Fig. 6).

After the larvae have forced their heads into the *stratum corneum* they continue the invasion by separating the stratified layers of the cells, Figs. 3, 4 and 5. On their way through the *stratum corneum* they were seen to advance and retreat several times. They remain in the *stratum corneum* for periods varying from a few minutes up to two hours and sometimes even longer. In the *stratum corneum* the larvae were found lying parallel to the surface of the skin (Fig. 3) in a position similar to that of hookworm larvae (*A. duodenale*) observed in a study of the original specimens prepared by Looss (1905) when he investigated the penetration of the skin by hookworm larvae. After resting in the *stratum corneum* the larvae make their way downwards into the epidermis. According to Taliaferro and Sarles (1939) the infective larvae seem to penetrate directly, and only occasionally utilize a hair follicle. Thereafter they were found in the loose subcutaneous tissue as in Fig. 7.

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Fig. 1.—Infective larvae in various attitudes on abdomen of young mouse. A. Almost vertical, as in Fig. 2. B. Lying on skin. C. Looped. Fig. 2.—Section of skin (mouse) with larva resting on skin by its tail, 15 minutes after exposure. (X. 66). Figs. 3, 4 and 5.—Sections of skin (rat) showing larvae having penetrated the cuticle, 30 minutes after exposure. (X. 470). Fig. 6.—Section of skin (rat) showing larva in hair follicle, 30 minutes after exposure. (X. 470). Fig. 7.—Section of skin (mouse) showing larva in loose connective tissue, 15 minutes after exposure. (X. 66). Fig. 8.—Dead larva in precucullary lymph gland of mouse. (X. 66).

To face p. 36.

**A New Tapeworm, *Diphyllbothrium salvelini* sp.
nov., from a Salmon, *Salvelinus alpinus*, in
Greenland**

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By kind permission of the Trustees of the British Museum (Natural History) the writer has had the opportunity of studying some tapeworms collected from a Greenland Salmon (*Salvelinus alpinus* subsp. ?) from Ottostrand, East Greenland, in August 1948 by Hjalmar Fleischer of Oslo. The material was found in the "gut" and contained about thirty specimens of an adult *Diphyllbothrium*, which appears to be new, along with specimens of *Diplocotyle olrikii* Krabbe, 1874 and *Eubothrium crassum* (Schränk, 1790). The material of the new form has been studied in whole mounts and several sets of serial sections.

Diphyllbothriidae Lühe, 1910.

Diphyllbothrium Cobbold, 1858.

Diphyllbothrium salvelini sp. nov.

These are medium-sized tapeworms. They measure more than 80 mm. in length and 2.1 mm. in maximum breadth. The oval scolex is about 1.16 mm. in length and 0.77 mm. in maximum width. It has well-developed bothria, formed by a pair of deep grooves which run the length of the scolex. In sections, the parenchyma is coarse with a glandular appearance. In a cross-section, the longitudinal muscles in the scolex are fairly conspicuous, consisting of four bands, two bands in the isthmus and the other two on the lateral edges at right angles to the former. There is no neck, for the scolex commonly overlaps the anterior segments. The latter are much wider than long, while the mature segments are square and the gravid segments longer than broad. The anterior segments broaden rapidly from the scolex backwards and are markedly craspedote. There is only one set of genitalia in each

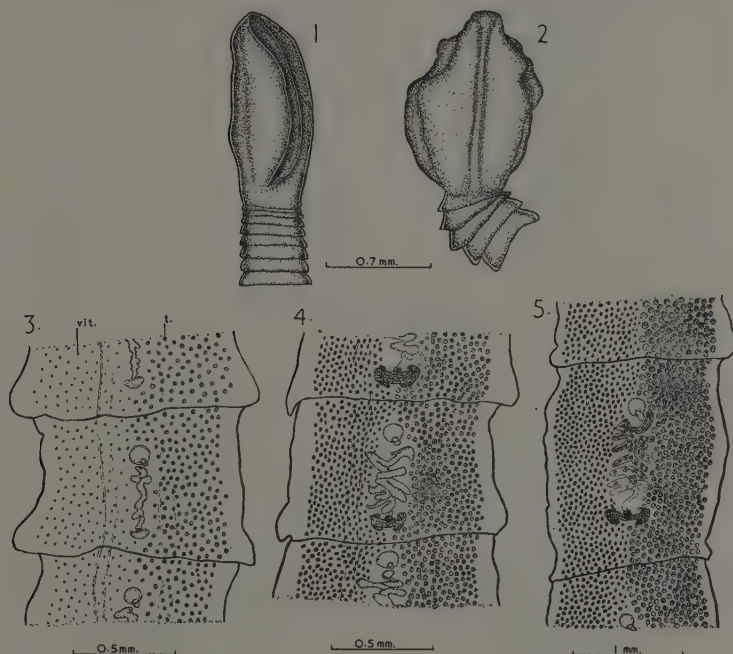
* L. S. Yeh.

segment. The cuticle is 0.007 mm. thick. The strong subcuticular layer measures 0.06 mm. in thickness. It is reinforced with scattered bundles of longitudinal muscles. There are three layers of longitudinal muscles. The first layer consists of minute fibres immediately under the cuticle. The second consists of weak and sparsely scattered groups, some lying in the subcuticular tissue, but most of them mainly between this tissue and the vitellaria. The parenchymal musculature is extremely well developed and consists of powerful longitudinal bundles closely packed into an almost continuous band. In a cross-section of a worm, measuring 0.5 mm. dorso-ventrally, the parenchymal longitudinal musculature measures 0.06 mm. in thickness. Its inner surface has a layer of circular muscle 0.015 mm. in thickness. There appear to be eight longitudinal excretory vessels running among the vitellaria in the cortex. They are so arranged that they divide the lateral halves of the worm into three equal portions. There is also another pair of very large longitudinal excretory tubes lying ventro-laterally in the medulla among the testes, slightly lateral to the ovary. Inside this large medullary tube there appears to be a net-work of delicate tissue.

The testes tend to be slightly ovoid, with their long axes dorso-ventral and rather constant in size, measuring 0.06×0.11 mm. There are about 400 per segment. They lie in a single layer in the medulla and are continuous from segment to segment. They are usually confluent in the anterior and posterior regions of the segments. In cross-section either at the anterior or posterior part of the segment, there is a maximum number of about 25 testes. In sagittal sections between the main excretory vessel and the lateral border of the body there is a maximum number of about 18 testes. The convoluted vas deferens lies median and dorsal to the uterus. The small seminal vesicle measures 0.08×0.09 mm. and enters the cirrus-sac dorso-posteriorly. The latter measures 0.18×0.28 mm. The coiled cirrus is slightly protruded in many of the whole mounts.

The genital atrium opens ventrally and usually in the first quarter of the segment. Like the ovary, its distance from the border appears to vary in different segments. The vaginal opening is situated immediately posterior to the male opening in the base of the genital atrium. The convoluted vagina remains median and ventral in its course to join the ovary, which is slender. The latter organ is H-shaped with a narrow isthmus and the posterior arms often meeting. It lies in the posterior fourth of the segment in the ventral half of the medulla and measures 0.45–0.50 mm. in width and 0.07–0.15 mm. in height. The vitelline

follicles appear to form a continuous field extending from segment to segment, and lie closely distributed in a single row within the cortex. Their continuous distribution is interrupted for a distance of about 0.22 mm. in the median plane, dorsally and ventrally, in the area between the ovary and cirrus-sac of each segment. The follicles also lie very closely to and often overlapping part of the uterus, ovary and genital



1.—Ventral view of scolex. 2.—Lateral view of scolex. 3–5.—Immature, mature and gravid segments.

pore, thus leaving no distinct space around these organs, as so frequently seen in the other species. The uterine loops are disposed as usual in the genus *Diphyllbothrium*. They reach the level of the cirrus-sac, but do not extend beyond or surround this structure. The number of loops varies with the age of the segment, but usually in a fully mature or gravid segment there are 6–8 loops on each side. The uterine pore is

ventral and slightly posterior to the aperture of the genital atrium. There are only a few eggs, and these are mostly packed in the anterior half of the uterus. The eggs are broadly ovoid, thin-shelled and operculate, measuring $36-40 \times 58-63$ microns.

Specific diagnosis : Diphylobothriidae Lühe, 1910. *Diphylobothrium* Cobbold, 1858, with generic characters. Body more than 80 mm. in length and 2.1 mm. in maximum breadth. Scolex well-developed, measuring 1.16 mm. in length and 0.77 mm. dorso-ventrally, with deep grooves. There is no neck. The strobila broadens rapidly backwards and the segments are markedly craspedote. Immature segments several times broader than long, mature segments square and gravid segments longer than broad. Only one set of genitalia per segment. Cuticle 0.007 mm. thick. Subcuticular layer 0.06 mm. thick. Parenchymal musculature well-developed, measuring 0.06 mm. in thickness. Its inner surface is reinforced with a layer of circular muscles. Testes 0.06-0.11 mm. oval, 400 per segment, disposed in a single layer in the parenchyma and are continuous from segment to segment. Maximum number of testes in cross-section about 25 and about 18 in sagittal section. Vas deferens convoluted, median and dorsal. Seminal vesicle 0.08×0.09 mm. and cirrus-sac 0.18×0.28 mm. Genital pore ventral, in first fourth of segment. Vagina ventral. Ovary in posterior fourth of segment, measuring $0.45-0.50 \times 0.07-0.15$ mm. Vitellaria continuous from segment to segment. In the anterior and posterior parts of the segment, they form a circular band in cross-section. But in the central parts of the segment this band is interrupted dorsally and ventrally. They invariably overlap part of the genitalia, leaving no clear surrounding space. Uterine pore slightly posterior to genital aperture. Uterine loops horizontal and balanced on each side, with 6-8 loops, never extending beyond or surrounding the cirrus-sac. Eggs fewer in number, ovoid, thin-shelled and operculated, measuring $36-40 \times 58-63$ microns.

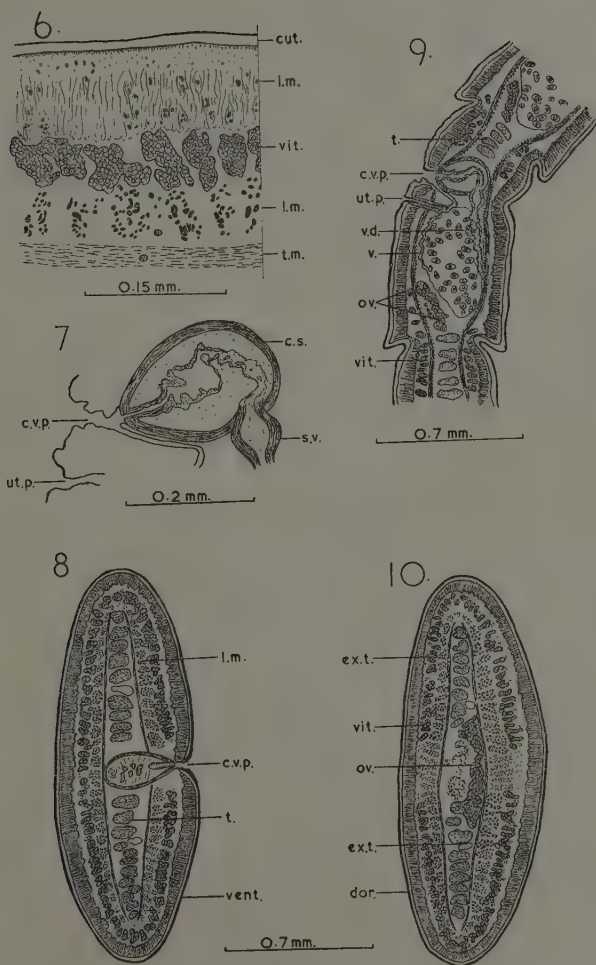
Host : *Salvelinus alpinus* subsp. ?

Locality : Ottostrand, East Greenland.

Co-types : In the collection of the British Museum (Natural History).

Abbreviations used in figures 6 to 10 :

C.s., cirrus-sac ; cut., cuticle ; c.v.p., genital pore ; dor., dorsal side ; ext., longitudinal excretory vessel ; l.m., longitudinal muscle ; ov., ovary ; s.v., seminal vesicle ; t., testis ; t.m., transverse muscle ; ut. p., uterine pore ; v., vagina ; vent., ventral side ; v.d., vas deferens ; vit., vitellaria.



6.—Transverse section of muscular system. 7.—Sagittal section of cirrus-sac.
 8.—Cross-section in vicinity of cirrus-sac. 9.—Median sagittal section of segment.
 10.—Cross-section in vicinity of ovary.

DISCUSSION.

It has generally been assumed that the genus *Diphyllobothrium* is peculiar to homoiothermal animals. As far as the writer is aware there has been only one report of this genus from poikilothermal animals, i.e. *Diphyllobothrium serpentis* Yamaguti, 1935, from a Chinese snake *Naja naja atra* from Taiwan. The present record is the first of a *Diphyllobothrium* species to be reported from a fish and the second from a poikilothermal animal. This record shows that *Diphyllobothrium* does not have restricted host-specificity as formerly thought. Markowski in his detailed study of the genus *Diphyllobothrium* from various animals has greatly reduced the number of species. From his work he has shown that the hosts are widely different and not closely related.

The writer feels convinced that *D. salvelini* is a "normal" parasite of *Salvelinus alpinus*, as its development appears quite normal. Moreover, along with the large number of *Diphyllobothrium* specimens, there were a number of *Diplocotyle olrikii* Krabbe, 1874, and *Eubothrium crassum* (Schränk, 1790) which are well-known parasites of *Salvelinus*.*

The scolex of *D. salvelini* in cross-section and longitudinal-section has a heavily granular gland-like tissue. Whether or not it is glandular does not affect the generic determination of the present species, as glandular tissue has been reported from many species of *Diphyllobothrium* by various authors, and Markowski (1952a) has shown that the genus *Glandicephalus*, which was originally erected by Fuhrmann on the presence of glands in the scolex, does not necessarily possess glands. Markowski recognises *Glandicephalus* on the grounds of "imbrication of the segments (.....); presence of a well-separated neck, and the arrangement of the musculature". The morphology of the present material agrees with the genus *Diphyllobothrium* in all respects.

The form described above does not seem to be identical with any of the previously known *Diphyllobothrium* spp., but appears more closely related to *Diphyllobothrium dendriticum* (Nitsch, 1824) (Syns. *D. laruei*, *D. oblongatum* etc. according to Markowski) than to any of the other species. There are, however, several important differences. In *D. salvelini* the shape of the scolex is very different, there is no neck, the genitalia are never duplicated in any of the segments, the number of testes in sections is very different especially in sagittal sections, in which

* The specimens *Diplocotyle olrikii* Krabbe, 1874, and *Eubothrium crassum* (Schränk, 1790) were identified by Mr. S. Prudhoe of the British Museum (Natural History).

the number is only one-half of that found in *D. dendriticum*, the vitellaria do not leave a clear space around the genitalia, the cirrus-sac is more anteriorly situated, and the uterus has only a few eggs.

ACKNOWLEDGMENTS.

The writer is grateful to Prof. J. J. C. Buckley under whose supervision this work was carried out. To Mr. S. Prudhoe he wishes to express his thanks for his kind help and for suggesting this examination and to Dr. S. Markowski for his critical discussions.

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**A New Bursate Nematode *Hepatojarakus malayae*
gen. et sp. nov. from the Liver of *Rattus rattus jarak*
(Bonhote) on Pulau Jarak, Straits of Malacca**

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A collection of parasitic worms was made from *Rattus rattus jarak* (Bonhote) from Pulau Jarak, "which lies in the middle of the Malacca Straits between Penang and Port Swettenham and some 85 miles from the Sembilan Islands opposite the Dindings." (Audy, 1950). It was collected by Dr. J. R. Audy, Senior Research Officer of the Division of Virus Research and Medical Zoology, Institute for Medical Research, Kuala Lumpur while investigating scrub-typhus on the island. The material was sent to Professor J. J. C. Buckley and was kindly made available to the present writer for fuller study.

On the basis of his preliminary study Professor J. J. C. Buckley (personal communication) expressed the view that the material probably represented an undescribed genus. Audy *et al.* (1950) have published a survey of Jarak Island with a provisional list of the helminths obtained from rats, based on Professor Buckley's identifications, and this has subsequently been quoted by Sandosham (1953). The detailed examination of the worms recovered from the liver carried out by the present author indeed indicated that the material belongs to a new genus. The name *Hepatojarakus malayae* is proposed.

These worms were recovered from two out of six rats. In one it was found in the biliary passages of the liver, and the other in a mass in the inferior vena cava. It appears rather unlikely that the latter is the usual habitat and more probable that the worms normally occur in the liver.

The worms are mostly male specimens, with only two females, one being immature. The state of preservation is fair, but not as good as

* L. S. Yeh.

could be desired. The worms are medium-sized with anterior ends attenuated. The cuticle has fine transverse striations. Laterally between the cuticular layers there is a mass of refractile globular granules which occupy more than half the length of the worm. The male measures 6.8–8.6 mm. in length by 0.21–0.27 mm. in width and the female 11.9 mm. by 0.23 mm. In the male, the oesophagus measures 0.38–0.42 mm. in length and the nerve-ring, cervical papillae and excretory pore are 0.18–0.22 mm., 0.22–0.24 mm., and 0.16–0.26 mm., respectively from the anterior end. The head is slightly inflated and has a number of cuticular striations. It has a diameter of about 0.05 mm. The oral opening is very peculiar. It has no lips, but is surrounded by a rudimentary corona radiata consisting of a group of about 16 elements. The buccal capsule is rudimentary and very inconspicuous. There appears to be an external circle of four papillae and two amphids.

Female: The following description was made from a single specimen not too well preserved. The vulva is about 3 mm. from the posterior end, the vagina is short and the ovejectors are short and divergent. The posterior branch of the ovary and uterus is confined to the caudal third of the worm. The conical tail measures 0.18 mm. in length and terminates in a spike. The eggs measure 62 by 37 microns.

Male: The bursa is well-developed and its inner surface has minute bosses. The rays are as follows: ventrals equal and parallel; externo-lateral slightly shorter and almost parallel to ventrals; medio-lateral and postero-lateral equal and parallel; externo-dorsal arising at origin of dorsal; dorsal bifurcate near its extremity, and each tip is bidigitate. The spicules measure 0.187–0.210 mm. in length. Each is split both anteriorly and posteriorly, giving the appearance of two unequal spicules fused together. The stouter and larger spicule has a hook near its distal end. The posterior extremity is unpigmented. There is a large spindle-shape gubernaculum almost half the length of the spicule, measuring 0.100–0.112 mm. long.

Host: *Rattus rattus jarak* (Bonhote).

Location: Biliary passages of liver.

Type locality: Pulau Jarak, Straits of Malacca.

Cotype: Deposited in the Department of Parasitology, London School of Hygiene and Tropical Medicine.

Generic diagnosis: (?) Trichostrongylidae. Lips absent, buccal cavity rudimentary or absent, oral opening surrounded by rudimentary external corona radiata. External circle of cephalic papillae appear to be four in number. Slight cephalic inflation present, with transverse striations. *Female:* Vulva in posterior half of worm. Two ovaries. Tail an elongated cone with one caudal spike. *Male:* Spicules split anteriorly and posteriorly; distal extremity with hook. Large gubernaculum present. Bursa with small bosses. Bursal rays well-developed. Ventrals equal and parallel. Externo-lateral slightly shorter than and almost parallel to ventrals. Medio-lateral and postero-lateral equal and parallel. Externo-dorsal arises at origin of dorsal. Dorsal bifurcate near its extremity and each tip is bidigitate.

Parasites of rodent tissue.

Genotype: *Hepatoharakus malayae* sp. nov.

Discussion: This parasite has a most interesting mouth opening. The buccal capsule is so rudimentary that it may be said to be absent. The mouth opening has no lips but a rudimentary external corona radiata with the leaf-elements forming a group of about 16. The Strongylidae have a well-developed chitinous buccal capsule and oral aperture usually surrounded by a corona radiata. The Trichostrongylidae may or may not have a rudimentary buccal capsule, but do not possess a corona radiata. The genus *Hepatoharakus* thus occupies an intermediate position between these two strongyloid families. But as the bursa and spicules are of the Trichostrongylid type we assign *Hepatoharakus* tentatively to this family. It appears that many of the trichostrongylid nematodes may fall into this group. The head-on view of *Allintoshius nycticeius* Chitwood, 1937 as figured by Chitwood for example, suggests a rudimentary leaf-crown. A more critical examination of a number of these genera will be necessary before regrouping can be effected.

Chen (1933) records a single female strongylid nematode from the liver of *Rattus rattus* in Canton. Unfortunately he gave no description of his specimen, so we are unable to say whether it belongs to *Hepatoharakus* or not. This is the only other record of which we are aware, of a strongyloid nematode in the liver of the common rat.

The genus *Hepatoharakus* resembles *Molineus* in many respects. It differs in the length of the externo-lateral ray which is as long as the other rays and runs parallel with the ventrals; the mouth opening is also different. *Hepatoharakus* appears to be related to many of the bat

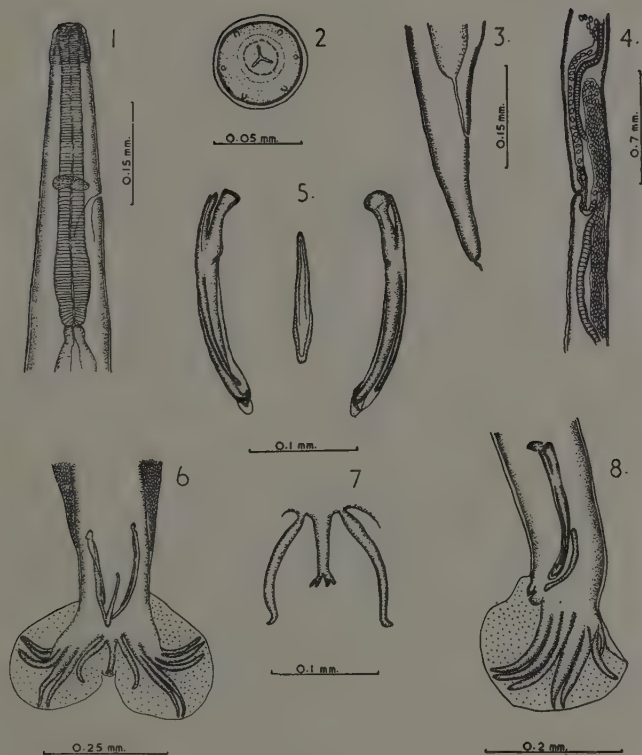


Fig. 1.—Anterior end of worm. Fig. 2.—End-on view of head. Fig. 3.—Tail of female. Fig. 4.—Vulval region of female. Fig. 5.—Spicules and gubernaculum. Fig. 6.—Dorsal view of male tail. Fig. 7.—Dorsal ray of bursa. Fig. 8.—Lateral view of male tail.

trichostrongylid nematodes but they are not sufficiently close to warrant any comparison.

Rictularia tani Hoeppli, 1929.

A large number of these worms were present in the collection. They agree very well with the original descriptions as given by Hoeppli (1929) and Chen (1936), with the exception that neither author described or figured the buccal teeth as being bifurcated. Each of the three teeth is bifurcated, so that three teeth point into the buccal capsule, and the other three point downwards into the oesophageal lumen.

ACKNOWLEDGMENTS.

The writer wishes to express his deepest gratitude to Professor J. J. C. Buckley who made the preliminary study of these worms and kindly made them available to the present writer for further examination. To Dr. P. L. leRoux, he is most grateful for his many helpful suggestions and criticisms.

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A New Method for the Production and Recovery of Cysts of Root Eelworms (*Heterodera* spp.) for Use in Bio-assay

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Eelworm cysts recovered from infested soil by the normal procedures of flotation and sieving have subsequently to be separated from plant and other debris which usually forms by far the larger proportion of the "float." Hatching tests carried out on whole floats are generally unsatisfactory, since the incubated debris forms a suitable substrate for the multiplication of micro-organisms which compete with the nematodes for the oxygen supply in the hatching fluid. Consequently larval emergence is often reduced or retarded, and extraction and estimation of the hatched larvae made more difficult (Table I). Multiplication of the micro-organisms may be prevented by the addition of traces of certain chemicals, e.g., copper sulphate, but the concentration required may reduce hatching of some populations of *Heterodera* (Fig. 1). Moreover, the use of such sterilizing agents is undesirable where artificial hatching media are being tested. By certain culture methods, very high populations of cyst-forming eelworms may be produced. In the field it is unusual to find more than 3 or 4 cysts per gram of soil. When peas were grown in an artificial field-plot consisting of a 6-in. layer of topsoil infested with pea eelworm (*Heterodera göttingiana* Liebscher) overlying uninfested subsoil, the eelworm population in the topsoil increased from 1 cyst (=100 eggs) to 10 cysts (=1,200 eggs) per gram of soil while the pea crop showed only slight symptoms of eelworm attack. Presumably the plants were able to thrive in such highly infested soil because the deeper roots escaped damage. When host plants were grown in infested soil in pots plunged in a potting mixture of steam-sterilized loam, horticultural peat and sand with the necessary minerals and fertilizers, some of the roots grew through the drainage holes in the pots into the rich soil below. Under these conditions the

roots within the pots could support very high numbers of cysts, especially under glasshouse conditions. In this way in a population of potato eelworm (*Heterodera rostochiensis* Woll.) as many as 80 cysts per gram of soil was produced (T. D. Williams, personal communication). The "float" from 2 of this soil, yielding 160 cysts with very little debris, could be used directly as a replicate in bio-assay.

TABLE I.

Beet eelworm (*Heterodera schachtii* Schm.): larval emergence from "clean" cysts (cysts alone) and "dirty" cysts (cysts plus debris) in swede leachings with and without copper sulphate.

| Treatment | Repl. | Cumulative Hatch (8 days) | (Larvae/100 g. soil sample) (32 days) |
|---------------------------|-------|------------------------------|---|
| 1. | 1 | 2040 | 2240 |
| "Clean" cysts in swede | 2 | 5425 | 6216 |
| leachings alone | 3 | 3400 | 3632 |
| | 4 | 3150 | 3296 |
| | Total | 14015 | 15384 |
| 2. | 1 | 3525 | 4485 |
| "Clean" cysts in swede | 2 | 4125 | 5660 |
| leachings plus 20 p.p.m. | 3 | 2550 | 2875 |
| Copper sulphate | 4 | 2400 | 3010 |
| | Total | 12600 | 16030 |
| 3. | 1 | 1260 | 2432 |
| "Dirty" cysts in swede | 2 | 1210 | 2157 |
| leachings alone | 3 | 1880 | 2500 |
| | 4 | 360 | 556 |
| | Total | 4710 | 7645 |
| 4. | 1 | 1060 | 1465 |
| "Dirty" cysts in swede | 2 | 1740 | 2550 |
| leachings plus 100 p.p.m. | 3 | 1110 | 2180 |
| copper sulphate | 4 | 2860 | 3960 |
| | Total | 6770 | 10155 |

The apparatus shown in Fig. 2 was designed to deal with such soil populations. It consists of 4 parts, part (A) being a funnel of sheet copper soldered to a cylindrical portion made from brass tubing; (B) and (C) are two sieves, made by soldering a circle of phosphor-bronze wire mesh into a section of brass tubing; and (D) a cylinder of solid brass, drilled and turned to the shape indicated. (A) and

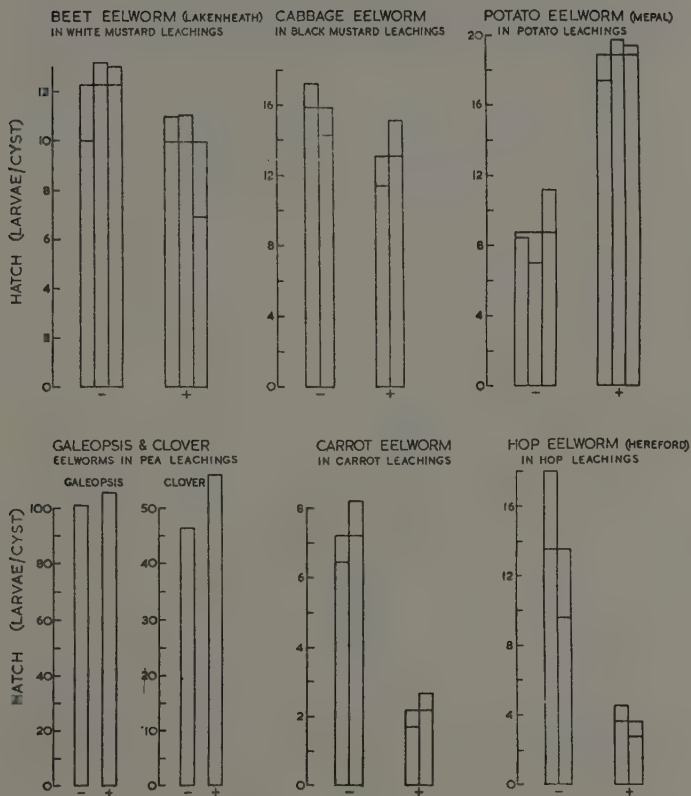


Fig. 1.—The effect on larval emergence from "clean" cysts of seven populations of *Heterodera*, of adding copper sulphate to the leachings. Hatch in leachings without copper sulphate (—) is compared with that in leachings with 20 p.p.m. copper sulphate (+), which is considered the minimum necessary to keep the hatching fluid reasonably free of fungi and other micro-organisms. Results are given for the beet, cabbage, potato, *Galeopsis*, clover, carrot and hop eelworms *H. schachtii*, *cruciferae*, *rostochiensis*, *galeopsidis*, *trifolii*, *carotae*, *humuli* respectively).

(D) are provided with milled collars (m) for convenience in handling. (C) fits neatly into (D) which in turn is a close push-fit into the lower end of (A). In use, the parts are fitted together as shown, the milled portion of (A) being held in the clamp of a retort stand. A length of rubber tubing (R) connects the lower end of (D) to a suction pump, which is kept going throughout the operation. (D) is lowered slightly so that the internal sloping surface of (C) is continuous with that of (A). A small sample of air-dry infested soil is weighed out and put up for flotation in a conical flask in the usual way. The "float" is

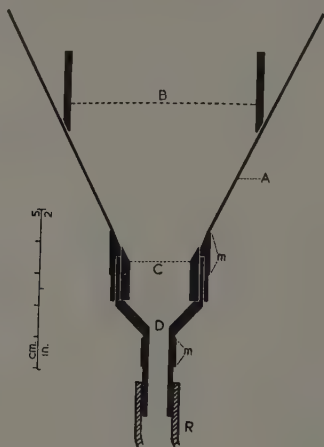


Fig. 2.—Apparatus for the recovery of eelworm cysts for use in bio-assay. For explanation see text.

then decanted into (B) and washed through with tap water. (B) is removed and the internal surface of (A) washed down gently. (D) is then withdrawn from (A), the small sieve (C) removed, and the cysts and debris washed from (C) into a solid watchglass. This can be done with 2–3 ml. of water from a washbottle.

In this or any cyst-sieving apparatus, the mesh used for upper and lower sieves may be varied, depending on the eelworm species and the purpose for which the cysts are required. For general purposes the writer uses a 20-mesh (28 S.W.G.) upper sieve and a 60-mesh (36 S.W.G.) lower sieve, as all eelworm cysts will pass through the former

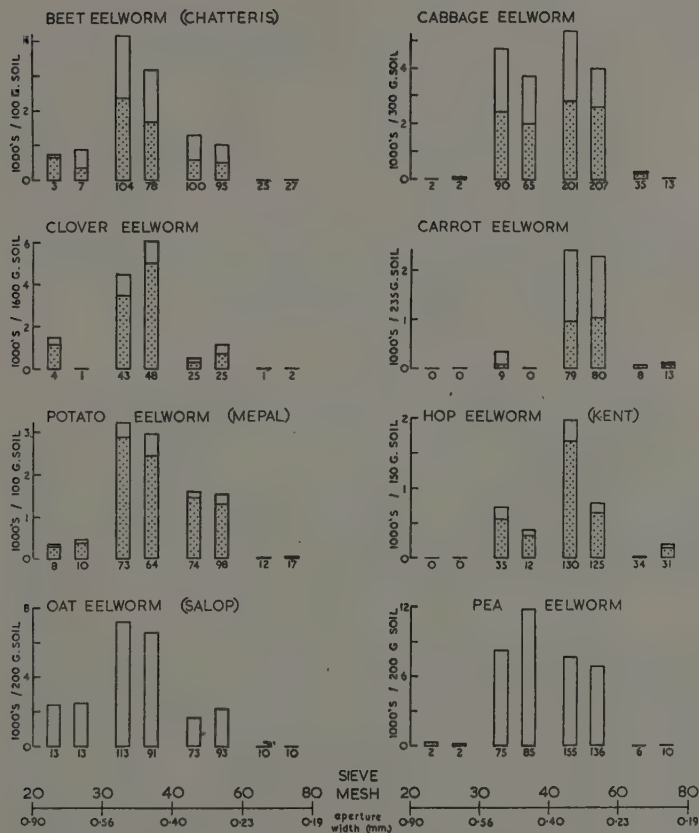


Fig. 3.—Eggs-and-larvae (heights of columns) and “hatchable” larvae (stippled) in the various fractions when cyst populations of *Heterodera* are washed through a series of sieves of decreasing aperture size. Two replicates of each population were used, each being separated by sieving into 4 fractions. The mesh and aperture size of the sieves limiting each fraction are indicated on the scale at the base of the figure. The number of cysts in each fraction is given beneath the appropriate column. Results are given for the beet, cabbage, clover, carrot, potato, hop, oat and pea eelworms *H. schachtii*, *cruciferae*, *trifolii*, *carotae*, *rostochiensis*, *humuli*, *major*, *göettingiana* respectively).

and all but a few of the smallest cysts are retained by the latter (See also Jones, 1945). For bio-assay purposes this sieve range can be narrowed so as to retain most of the eelworm content of the sample while rejecting much of the debris. This results in cysts more even in size, therefore more suitable for bio-assay experiments. When soil samples from 8 field populations of root eelworms were subjected to flotation and the "floats" washed through a sequence of 5 sieves of decreasing aperture size (Fig. 3), most of the "hatchable" larvae and total eggs and larvae were contained in one or two of the four cyst fractions resulting. Thus for bio-assay purposes, an upper sieve of 30-mesh and a lower sieve of 40-mesh would be ideal for the 4 populations shown on the left side of the figure, while 30-mesh and 60-mesh would serve for the remaining 4 populations.

SUMMARY.

Methods are discussed for greatly increasing the cyst content of *Heterodera*-infested soil, so that very little soil need be "floated" to provide the number of cysts necessary to form a replicate in bio-assay. Such a "float" contains very little debris and may be used directly, thus avoiding the laborious and time-consuming step of separating the cysts from the debris. An apparatus for quick recovery of the "float" is described.

ACKNOWLEDGMENTS

I wish to thank my colleagues in the School of Agriculture for assisting in the work, especially Messrs. F. G. W. Jones and T. D. Williams for their interest and advice, and Messrs. R. Day and P. Halfpenny for technical assistance. The work was financed by the Sugar Beet Research and Education Committee.

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****Nematobothrium labeonis* n.sp., a Member of the
Family Didymozoidae (Trematoda) from a
Freshwater Fish**

By W. F. J. McCLELLAND, M.Sc.

*From the Department of Parasitology, London School of
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The material described in this paper was collected in the course of a survey of Nile fish carried out in the Department of Zoology, University College, Khartoum, and was sent to the London School of Hygiene and Tropical Medicine. It consisted originally of seven sexually mature and three immature specimens stained with carmine and mounted in Canada balsam, as well as a number of specimens preserved in glycerine alcohol. Several of the latter were stained with Ehrlich's haematoxylin or paracarmine and mounted, while the remainder were used in an unsuccessful attempt to cut transverse sections. The description which follows is based on the examination and measurement of thirteen whole mounts of sexually mature worms. All these specimens were obtained from species of *Labeo*, a freshwater fish taken in the Nile at Khartoum. Two specimens were from *Labeo coubie*, and the remainder from *L. horie*. In addition, one immature specimen was recovered from *L. niloticus*.

Later, in response to a request for more specimens, a quantity of fresh material was provided from the same three hosts. This was preserved in formalin and used for the preparation of transverse sections of the anterior and posterior extremities of the body and of the region of the ootype.

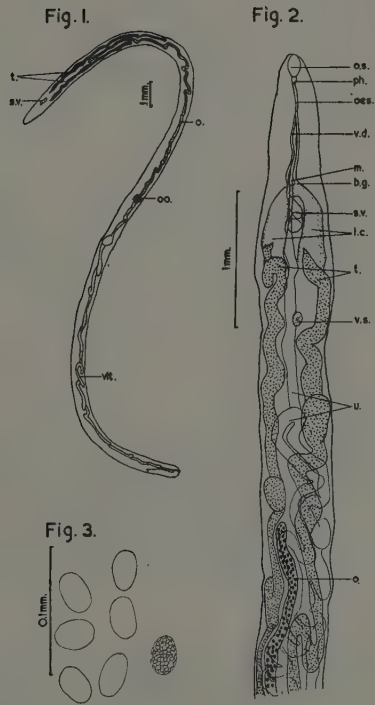
* Part of a thesis approved by the University of London for the award of the M.Sc. degree.

The position of the parasites within the host is noteworthy. Almost all the species ascribed to the genus *Nematobothrium* from time to time are known to occur encysted on the gills, gill-covers or the bones of the head of marine fishes and, indeed, the majority of members of the family Didymozoidae are found in similar positions. The two other species placed in the subgenus *Maclarenozoum*, *Nematobothrium molae* Maclaren, 1903 and *N. lampridis* Yamaguti, 1940, were found encysted on the gills of *Orthogoriscus mola* and *Lampris regia* respectively. The material described herein, however, was found within the orbit of the three species of *Labeo* mentioned. The individual worms were not encysted, but described as writhing actively within the orbit and easily collected after removal of the eyeball. The other species which has been found free in the host's tissues is the form described by Moniez (1891) as *N. guernei* which occurred in cysts on the gills and free with one end attached to the inferior maxillary muscles of *Germo alalonga* (= *Thunnus alalonga*) and also in the intestine. The species described in this paper is, however, the first member of the genus and apparently only the second member of the family to be found parasitizing a freshwater fish.

Nematobothrium (Maclarenozoum) labeonis n. sp.

The body is filiform, 14.6–28.6 mm. long with a maximum breadth of only 0.89–0.70 mm. The posterior extremity is bluntly rounded and the anterior region tapers to a blunt termination. Some specimens exhibit a slight constriction a short distance behind the anterior extremity, but most of them have no such clearly defined neck region. The maximum breadth is attained at any point posterior to the tapering anterior end of the worm, but frequently occurs near the posterior end.

The mouth is anterior and terminal in position, surrounded by a lemon-shaped sucker having a length of 0.09–0.14 mm. and a maximum breadth of 0.06–0.09 mm. Immediately behind the sucker is an insignificant pharynx 0.015–0.05 mm. long and 0.015–0.05 mm. in diameter, followed by a narrow, slightly undulating oesophagus, 0.52–0.97 mm. long, which divides to form two caeca running posteriorly at least as far as the posterior end of the ovary. Transverse sections of the posterior end of the body indicate that posterior to the ootype the two gut caeca unite or that one terminates some distance in front of the posterior extremity of the body, while the other extends to the posterior end of the body where it ends blindly. The diameter



Nematobothrium labeonis n. sp.

Fig. 1.—Whole mount showing disposition of testes, ovary and vitellarium (semi-diagrammatic). Fig. 2.—Anterior end of body. Fig. 3.—Eggs, with sculpturing on shell added in one specimen.

of the caeca is not constant, but increases and decreases along the length of the worm.

A very small ventral sucker lies 1.38–1.94 mm. from the anterior end of the body. In surface view it is oval in outline, 0.07–0.11 mm. long and 0.06–0.08 mm. broad, with a depth of about 0.07 mm. The sucker is so small that it might easily be overlooked.

Apart from young specimens in which no sexual organs could be seen, the male and female reproductive systems were equally well developed in each worm and no evidence was found of the predominance of one sex over the other in individual worms, which occurs in some members of the family Didymozoidae. The testes, ovary and vitellarium are all cord-like structures which are usually looped or much convoluted, and often twisted with one another or with the loops of the uterus to such an extent that it is impossible to measure their actual lengths. The sizes of these organs have therefore been expressed as the length of the worm occupied by each.

The testes are paired and lie in the anterior part of the body, commencing between the bifurcation of the gut and the ventral sucker, and occupying 1.96–6.25 mm. of the body. The actual length of the testes is considerably greater. Thus, in one specimen 14.6 mm. long, the testes occupied 1.96 mm. of the body length, but the actual lengths of the testes were 2.54 and 2.48 mm. In another specimen which was damaged posteriorly and had a length of slightly more than 26.5 mm. The length of the body occupied by the testes was 6.25 mm. and the actual lengths of the testes were 8.55 and 7.35 mm.

From the anterior end of each testis a vas efferens runs forwards. These two ducts join to form a coiled seminal vesicle just posterior to the bifurcation of the gut, and a narrow vas deferens originating at the anterior end of the seminal vesicle follows a straight or slightly sinuous course anteriorly to open into the uterus immediately before the latter opens at the genital aperture close to the sucker.

Abbreviations used in Figs. 1–4.

b.g. = bifurcation of gut; **e.c.** = excretory canal; **g.p.** = genital aperture; **i.c.** = intestinal caeca; **m.** = metraterm; **o.** = ovary; **oes.** = oesophagus; **oo.** = ootype; **o.s.** = oral sucker; **ph.** = pharynx; **r.s.** = receptaculum seminis; **s.v.** = seminal vesicle; **t.** = testes; **u.** = uterus; **v.d.** = vas deferens; **v.e.** = vasa efferentia; **vit.** = vitellarium; **v.s.** = ventral sucker.

Fig. 4.

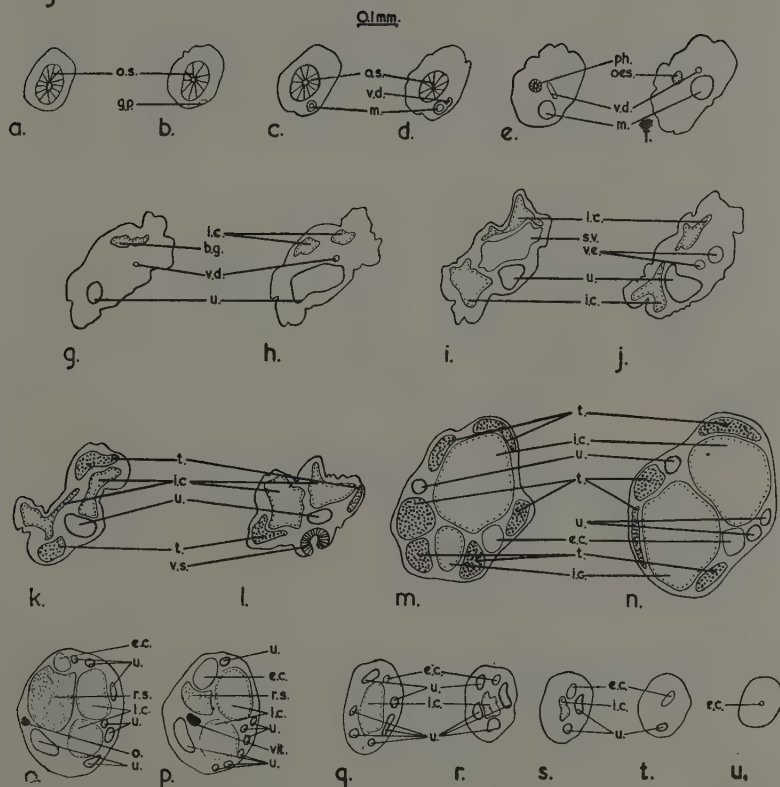
*Nematobothrium labeonis* n. sp.

Fig. 4.—Diagrams based on camera lucida drawings of serial transverse sections of the body. a-n. Anterior part. o.p. Region of ootype. q-u. Posterior extremity of body.

The single ovary occupies 3.40–10.0 mm. of the body length and is 0.043–0.097 mm. in diameter. The anterior end is usually slightly in front of the posterior end of the testes, a distance of 3.1–4.8 mm. from the anterior end of the body. The ovary is invariably very much convoluted. In two specimens 14.6 and 26.5 mm. long the ovaries occupied 4.1 and 10.0 mm. respectively of the body length but their actual lengths were 10.0 and 21.1 mm. respectively.

The ootype occurs between the posterior end of the ovary and the anterior end of the vitellarium at a distance of 7.0–13.8 mm. from the anterior end of the body.

A large vesicle was observed between the ovary and vitellarium. The nature of this structure was in doubt for some time, but, using an oil immersion objective, it was seen that the contents resembled the spermatozoa observed in sections of testis. It would therefore appear that this vesicle is a receptaculum seminis, but it was not possible to determine its relationship to the adjacent organs to settle the matter beyond doubt. No Laurer's canal was observed.

The uterus commences close to the ootype and appears to run anteriorly to a point between the anterior end of the ovary and the ventral sucker where it turns back, extending to the posterior end of the body, to turn forwards once again and run to the genital aperture close to the mouth; but the many convolutions make it difficult to determine the exact course of the uterus.

The eggs are produced in vast numbers and entirely fill the uterus in mature specimens. They are oval to subspherical in outline and non-operculate, measuring $0.031\text{--}0.036 \times 0.020\text{--}0.025$ mm. The shells are delicately sculptured.

At the posterior end of the body is a small longitudinal duct opening terminally and running longitudinally along the body. A small longitudinal duct was also observed in a ventral position commencing posterior to the ventral sucker. These structures were thought to be parts of a longitudinal excretory canal but it was not possible to identify the excretory system more definitely.

Type specimens are deposited in the Helminthological Collection of the London School of Hygiene and Tropical Medicine.

SYSTEMATIC POSITION.

The systematics of the family Didymozoidae are in a state of considerable confusion, for, although some of the forms included therein have been known for almost a century, many of the earlier descriptions of these worms are noteworthy for their inadequacy. Another difficulty is that although more extreme differences in form and structure are to be found in almost no other trematode family, the gradation from one individual form to another is often very slight. Thus, the delimitation and definition of genera is not at all easy.

The classificatory scheme proposed by Ishii (1935) is the most comprehensive one available and, bearing in mind the fact that the entire system is liable to drastic modification with extensions of knowledge of the group, the genus *Nematobothrium* is accepted here as including the species placed in it by Ishii, but subject to the modifications of nomenclature listed by Dollfus (1935), Baylis (1938) and Yamaguti (1938), and the addition of another species, *N. lampridis*, by Yamaguti (1940).

Ishii divided the genus into two subgenera according to the absence or presence of a ventral sucker. Maclaren (1904) suggested when he described *N. molae*, that a ventral sucker may have been overlooked when *N. filarina* van Beneden, 1858, and *N. guernei* Moniez, 1890 were described. In view of the incomplete nature of these descriptions, this may be true, but in the light of present knowledge, the division of the genus is convenient because it separates the forms known to possess a ventral sucker from those in which such a structure does not exist or has never been seen, and because the subgenus *Nematobothrium* contains forms which may not be congeneric.

The species described above has a very small but distinct ventral sucker, so that its position in Ishii's classificatory system is :—

Family : Didymozoidae Ishii, 1935 (= *Didymozoidae* Poche, 1926).

Subfamily : *Nematobothriinae* Ishii, 1935.

Genus : *Nematobothrium* van Beneden, 1858.

Subgenus : *Maclarenozoum* Ishii, 1935.

RELATIONSHIPS.

Although the new species described above has been placed in the genus *Nematobothrium* it is by no means certain that it is congeneric with all the species placed in that genus from time to time. However, *N. labeonis* does show a considerable similarity to *N. mola* MacIaren, 1903 and *N. lampridis* Yamaguti, 1940. On the other hand, there are differences which justify the separation of the three as distinct species. The principal differences involve the ventral sucker, the intestinal caeca and the vitellaria.

N. mola has a small ventral sucker lying between the intestinal bifurcation and the anterior ends of the testes. This feature is quite clearly shown by MacIaren's diagrams of serial transverse sections, as the section showing the ventral sucker also shows the vasa efferentia. In *N. labeonis* the ventral sucker lies posterior to the anterior ends of the testes so that the sucker and the testes occur in the same section. MacIaren found that the intestinal caeca of *N. mola* extend for only a short distance behind the bifurcation of the gut whereas in *N. labeonis* both caeca extend at least as far as the ootype and one extends to the extreme posterior end of the body. *N. mola* has paired vitellaria, but *N. labeonis* only one. The two species show lesser differences in the size of the oral and ventral suckers, and in host.

N. labeonis shows a much greater degree of similarity to *N. lampridis*. The form of the testes, ovary, vitellarium and uterus is similar; there is a single vitellarium in each species; and it is probable that both possess a receptaculum seminis. However, the two differ in several respects. *N. lampridis* is clearly divided into a forebody and hindbody, a condition not usually apparent in the case of *N. labeonis*. *N. lampridis* has a ventral sucker which appears from Yamaguti's fig. 47 to lie anterior to the anterior end of the testes, unlike the ventral sucker of *N. labeonis*. There is also a considerable difference in the size of the eggs in the two species, those of *N. lampridis* measuring $0.015-0.017 \times 0.011-0.012$ mm. while *N. labeonis* has eggs which are about twice this size, $0.031-0.036 \times 0.020-0.025$ mm. Lesser differences are the size of the ventral sucker and the thickness of the intestinal caeca immediately posterior to the bifurcation of the gut.

N. mola was found encysted in pairs on the gills of *Orthogoriscus mola* and *N. lampridis* occurred encysted in pairs on the gills of *Lampris regia*, both hosts being marine fishes. Most members of the family Didymozoidae occur under such conditions. *N. labeonis*

occurs in an unusual position in an unusual host. No other member of the genus *Nematobothrium* has ever been found free living in the orbit and only one other member of the family Didymozoidae has been found in such a position. Yamaguti (1936) described *Philopinna higai*, a parasite of the fins and, to a less extent, the orbit of the Japanese freshwater fish *Sarcocheilichthys variegatus*, but this parasite which is smaller and dorso-ventrally flattened, and generally of much more conventional trematode shape, is quite distinguishable from *Nematobothrium labeonis* which is believed to be only the second member of the family to be reported from a freshwater fish.

SUMMARY.

1. *Nematobothrium labeonis* n. sp. from the orbit of three species of *Labeo* is described.
2. The more recent literature relating to the classification of the genus is considered.
3. *N. labeonis* is contrasted with related species.

ACKNOWLEDGMENTS.

The work incorporated in this paper was carried out under the supervision and guidance of Professor J. J. C. Buckley. The original material was provided by Professor H. Sandon, University College, Khartoum, who most kindly sent fresh specimens at a later date, and provided encouragement during the course of the work. Mr. S. Prudhoe of the British Museum (Natural History) rendered great assistance by the loan of literature.

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A Redescription of *Aphelenchoides parietinus* (Bastian, 1865) Steiner, 1932

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In his "Monograph on the *Anguillulidae*, or Free Nematoids, Marine, Land and Freshwater; with Descriptions of 100 New Species," published in 1865, Bastian described a nematode which he found in the yellow lichen *Xanthoria* (then known as *Parmelia*) *parietina*. He named it *Aphelenchus parietinus*, giving a short description and two drawings. His drawings are reproduced in Fig. 1 and his description is as follows:

"Female, length $1/36$ ", breadth $1/833$ ".

External characters—Body pellucid, tapering very slightly forwards, but to a point backwards, where it appears to terminate in a sucker. Head almost truncate. Transverse striae $1/30000$ " apart.

Spear simple, $1/2000$ " long. *Oesophagus* $1/11$ th of total length; terminal swelling $1/2000$ " in diameter.

Intestine covered by a few scattered granules; internal tube well seen. *Anus* $1/770$ " from posterior extremity.

Vulva at commencement of posterior third of body.

Excretory duct opening at $1/266$ " from anterior extremity.

Male not seen.

Hab. with *Plectus parietinus*, in patches of yellow lichen (*Parmelia parietina*), Broadmoor, Berks."

In the same Monograph Bastian described *Aphelenchus avenae* which, according to Stiles and Hassall (1905), he made the type species of the genus: this was before the male was known. When Steiner, in 1931, found males of *A. avenae* and observed that they had a bursa and characteristic spicules, he removed all the other species until then included in *Aphelenchus* (including *A. parietinus*) to the subgenus

Pathoaphelenchus (Cobb, 1927) which he raised to generic rank. However, in 1932 he pointed out that *Aphelenchoides kühnii*, a new genus and species made by Fischer in 1894, was, in his opinion, identical with Bastian's *Aphelenchus parietinus*. Since Fischer's genus antedated Cobb's *Pathoaphelenchus*, the correct name of Bastian's species became *Aphelenchoides parietinus* (Bastian, 1865) Steiner, 1932. This is the type species of the genus *Aphelenchoides*, since Fischer's genus was monotypic.

Nematodes identified as *A. parietinus* have frequently been recorded from diseased and rotting plant materials and from soil, but owing to the inadequacy of Bastian's original description of the species, and to the fact that he found no males, the identification is often doubtful. This is well illustrated by the numbers of "new species" of *Aphelenchoides* which have been made only to be synonymized later with *A. parietinus*. Goodey (1951) gives a list of 13 synonyms of this species, and Micoletzky (1922) says that it has been described under no fewer than 14 names. The latter refers to it as the most variable of free-living nematodes and divides it into varieties *tubifer* and *microtubifer*; the varieties he separates into forms *parvus* and *magnus*, and these into sub-forms *informis* and *gracilis*. This classification is not in general use, but the fact that it was found possible and even desirable to make it illustrates the great variability of the species as at present understood.

The characters which have led so many authors to name new species have chiefly been differences in size and proportions of the body and the presence or absence of basal knobs on the stylet. In table 1 are summarized some of the different measurements given in the literature for species which have since been synonymized with *A. parietinus*. As regards the stylet, Bastian described it as "simple," and figured it without knobs (Fig. 1a). He coined the name *Aphelenchus* from two Greek words meaning "simple" and "spear" as opposed to *Tylenchus* meaning "knobbed spear". It seems likely that basal thickenings were present in the specimens he examined but were not sufficiently conspicuous for him to observe with the optical equipment which he used. Fischer, on the other hand, described the stylet of *Aphelenchoides kühnii* as distinctly knobbed ("deutlich knollig verdickt"), and showed it so in his drawing reproduced in Fig. 2a. Micoletzky found it to be variable—weakly knobbed ("schwach geknöpft") in 33 specimens, fairly distinctly knobbed ("mitteldeutlich geknöpft") in 7 and very distinctly knobbed

("sehr deutlich geknöpft") in 2 specimens. Goodey (1951) described and figured it with distinct, though small, knobs. Both dimensions and stylet are thus very variable in the published descriptions of

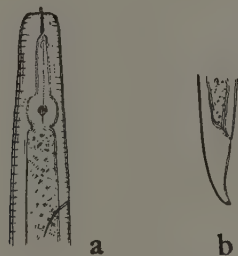


Fig. 1.—Enlarged copy of Bastian's figures of *Aphelenchus parietinus*. (a) Anterior extremity of female. (Plate 10, no. 102) (b) Posterior extremity of female. (Plate 10, no. 103).

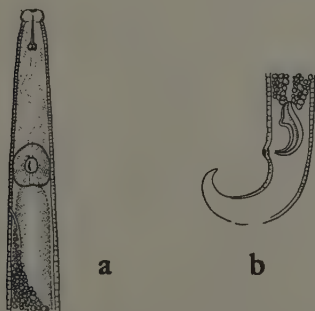


Fig. 2.—Copy of Fischer's figures of *Aphelenchoides hübnii*. (a) Anterior end of female, from plate 1, no. 2. (b) Tail end of male, from plate 1, no. 3.

nematodes which have been called *A. parietinus*. It appears possible that some populations might justifiably be described as separate species but before this can be attempted it is necessary to have an adequate description of the true *A. parietinus*.

It is most unlikely that Bastian left any preserved specimens which could be considered as types of his species, since nematology was not his chief study. He was primarily a physician specializing in nervous diseases, and was regarded as a pioneer in neurology. After publishing four papers on "Nematoids" between 1865 and 1868 when at the start of his medical career, he appears to have dropped the subject altogether. *A. parietinus* cannot therefore be re-described from the original material and the best that can be done is to examine nematodes from as nearly as possible the same source.

Several collections of yellow lichen from the locality where Bastian made his collections have therefore been made by the present writer during the past four years. Some came from the walls of a farmyard at Broadmoor, and others, through the courtesy and ready help of the Medical Superintendent, from the walls of the Broadmoor Institution which was probably standing in Bastian's days. The yellow lichen has been identified as *Xanthoria* (formerly known as *Parmelia*) *parietina*. When soaked in water it yielded numbers of nematodes and amongst these, on two or three occasions, were females of a species of *Aphelenchoides* which resembled that named by Bastian *Aphelenchus parietinus*. Whenever these were found a very careful search was made for males, but without success, and since the females never showed evidence of having been spermatized it appears that in this habitat males do not occur. This is unfortunate in a species which has been designated the type of its genus, as was proved in the case of *Aphelenchus avenae*, but as the female is very much like several of the other species of *Aphelenchoides* in general characters, it seems unlikely that the male, if it exists, will prove to be anomalous.

Aphelenchoides parietinus (Bastian, 1865) Steiner, 1932.

| Female | S.D. |
|---------------------|------|
| Length: 450.8 μ | 41.7 |
| Breadth: 17.2 μ | 1.43 |
| <i>a</i> 26.8 | |
| <i>b</i> 7.8 | |
| <i>c</i> 13.8 | |
| V 68% | |
| Tail 32.9 μ | 2.8 |

(Measurements are means of 50 (except tails, of which 49 were measured) made on specimens killed by gentle heat and fixed in 5 per cent. formalin.)

The cuticle, except on the head, is annulated, the annules being about 1–1.3 μ apart in the mid-body region. The lateral field (Fig. 3b) bears four equally-spaced longitudinal incisures which, shortly behind the oesophageal region and at the beginning of the tail, are reduced in number first to three, then to one which finally disappears. No deirid could be seen and phasmids were observed only with difficulty. The body tapers gradually towards the head which is distinctly offset, the sides being convex but slightly less so than in *A. ritzema-bosi*. There appear to be no superficial longitudinal marks on the head indicating the lip divisions, such as have sometimes been represented in drawings of the nematode. A face view of the head seen by incident light shows six lips, but papillae are not visible and the amphidial openings are not at all clear. The excretory pore is on the ventral surface close behind the oesophageal bulb, but no hemizonid could be seen. The anus is distinct and behind it the tail tapers fairly rapidly to end in a mucro which is usually a simple spike but may be somewhat truncate. When the nematode is killed by gentle heat the tail curves ventrally in a characteristic way approaching the form typical of the male of *A. fragariae*. The vulva is situated at two-thirds of the total length from the head: it is a simple transverse slit.

The stylet is 11–13 μ long (average of 8=11.75 μ) and is distinctly thickened at the base, the thickenings being smaller than the knobs of *A. ritzema-bosi* and *A. blastophthorus* and not so sharply offset. A guide ring surrounds the tip of the stylet, appearing star-shaped when seen from the front and as two short rods when seen from the side (Figs. 3d and e). The first region of the oesophagus is narrow with a well marked lumen and is followed by a prominent median bulb occupying about two-thirds of the width of the body at the same point. The bulb is longer than broad and slightly wider at the posterior than at the anterior end. In the centre there is a conspicuous valve with crescentic thickenings. A duct from the oesophageal gland opens into the lumen just in front of the valve and two other ducts presumably enter behind it in a ventrolateral plane, since occasionally it is possible to see a break in the wall of the lumen at this point (Fig. 3c). The elongated oesophageal gland is in length about four times the greatest body width and lies dorsally along the intestine, closely adpressed but separate from it. The intestine begins immediately behind the oesophageal bulb as a tube about one quarter to one-third the width of the bulb and, gradually widening, runs straight to the narrow rectum which has a length equal to about twice the anal body-width.

The intestine walls are usually well stocked with oil globules. The nerve ring surrounds the intestine and oesophageal gland close behind the median bulb.

The ovary is straight and consists of a single row of about a dozen oocytes, the tip usually lying a short distance behind the end of the oesophageal gland but sometimes overlapping it. The oviduct is short and in a few specimens a single egg was seen in the uterus. The egg is about 4 times as long as it is broad. There is a small post-vulval sac, usually about 2 body widths long, but neither here nor in the uterus could sperms be seen.

No males have been found.

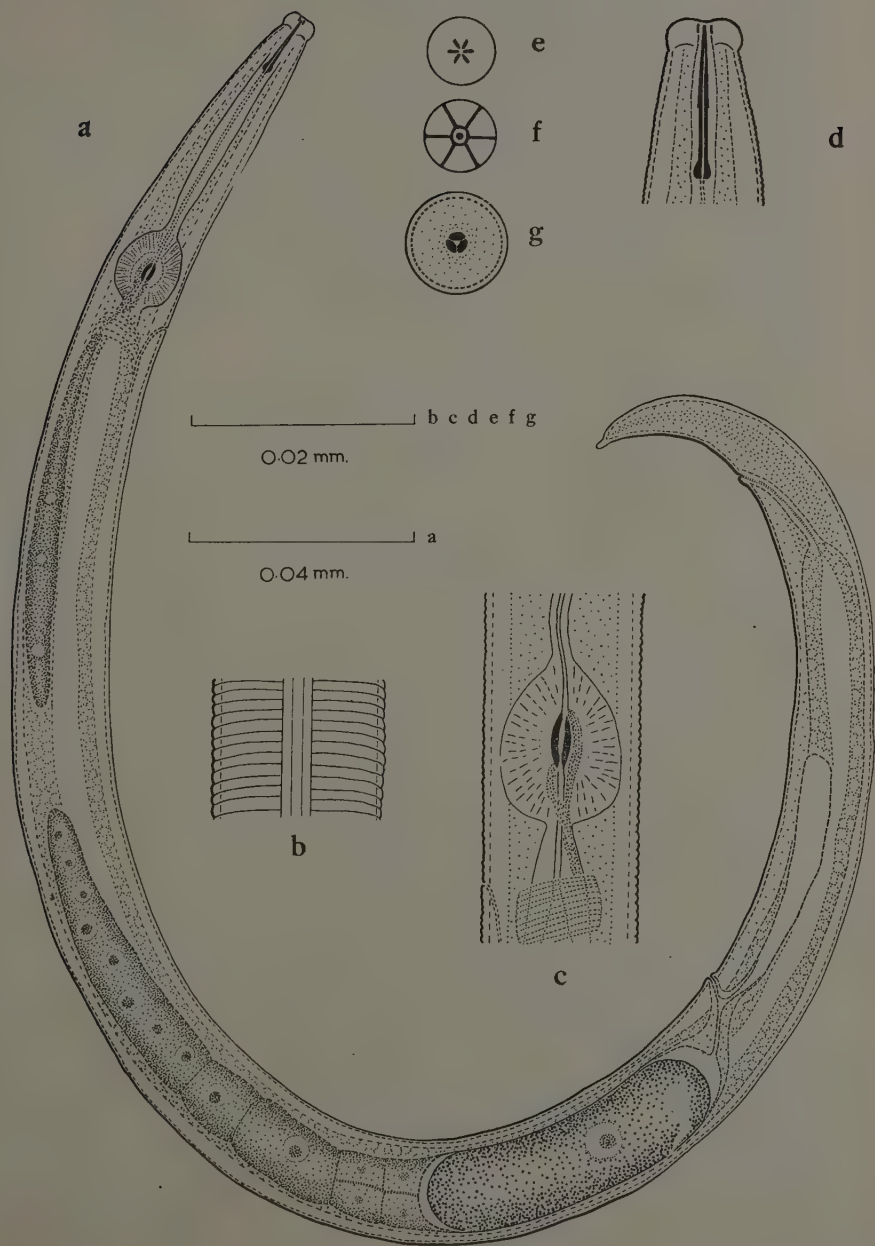
Bionomics.

A. parietinus is a common inhabitant of *Xanthoria parietina* and has also been found in the green foliose species *Cladonia fimbriata* var. *simplex*. Within the lichens it must be able to withstand considerable desiccation. On the assumption that it feeds on the fungal constituent of the lichen attempts were made to culture it with a fungus on agar plates. On one occasion females, eggs and larvae were found after a period of about three months, but there was no sign of males. It seems probable that this species is mycophagous.

The species herein described and identified as *Aphelenchoides parietinus* (Bastian, 1865) Steiner, 1932, can be distinguished from other species of the genus by its small size and relative plumpness, by the well developed stylet with distinct basal thickenings and by the form of the tail with its simple mucro. Differences between *A. parietinus* and some similar species are listed in table 2, the characters distinguishing a species from *A. parietinus* being printed in heavy type. All species except *A. latus* differ markedly in length, and although this is not a good specific character since it could vary with habitat, in all cases there is at least one other obvious difference such as relative width, mucro or stylet.

Reference to table 1 giving measurements of some of the species which have been synonymized with *A. parietinus* shows that considerably greater values are given for the length of most of the species

Fig. 3.—*Aphelenchoides parietinus* from present observations. (a) Whole female. (b) Lateral field in mid-body region. (c) Oesophageal bulb, nerve ring and excretory pore. (d) Head to show stylet. (e), (f), (g) Diagrammatic optical sections of head showing skeletal structure and spear base (g).



than have been found by the present writer. This is very noticeable in Bastian's description of *A. parietinus*. His measurements are given in fractions of an inch and it seems possible that the discrepancy is due to differences in technique. To take another example, the value he gives for the length of *Aphelenchus avenae*, described in the same Monograph, is $1/20''$ ($=1.27$ mm.), but the female of this species is now known to be 0.8–0.95 mm. long (Goodey 1951). Both in this species and in *A. parietinus* the values given by Bastian are about four-thirds of the values now accepted, which supports the view that the difference is one of technique and the nematode he described is in each case the same as that now recognised as *Aphelenchus avenae* or *Aphelenchoides parietinus* respectively.

It is possible that some of the other "species" which have been synonymized with *A. parietinus* since their description under different names should in fact be considered as distinct species. For instance, Fischer's *Aphelenchoides kühnii* differs considerably from *A. parietinus* as it is here described: it is one and a half times as long and distinctly more slender in proportion (a is 32 as compared with 26 in *A. parietinus*), while the stylet is $14\ \mu$ as compared with $11.75\ \mu$ and, according to Fischer's drawings, it has more pronounced knobs. Too much reliance cannot, however, be placed on the illustrations: for example, in Fischer's Fig. 1 showing the whole worm, if the vulva and anus be taken as ventral, the oesophageal gland is also ventral and the excretory pore is dorsal. To the present writer it seems highly doubtful that *A. kühnii* is identical with *A. parietinus*, but it is extremely difficult to be sure in the absence of the original specimens. Similar doubts arise if one examines Ritzema Bos's description of *Aphelenchus ormerodis* which has also been synonymized with *A. parietinus*. He found the nematodes which he described under this name in strawberry plants together with *A. fragariae*. The impression given by his drawings of *A. ormerodis* is that the nematode he was describing was what is now known as *Aphelenchoides ritzema-bosi*, and according to our present knowledge this species might well have been present in the strawberry plants he was examining. However, according to Ritzema Bos, the stylet of *A. ormerodis* does not have definite knobs, although it is somewhat thickened at the posterior end. But in his drawings the male at least appears to have a knobbed stylet. A great deal evidently depends on the individual observer's conception of the difference between "knobbed" and "thickened". Since the situation is obviously very nebulous it seems better, unless and until further

TABLE I.
Some nematodes which have been synonymized with *A. parietinus*
(arranged in descending order of length of female)

| | Author | Females | | Males | | Stylet μ |
|----------------------------------|------------------|---------------------------|-----------------|--------|---------------------------|------------------|
| | | Length (mm.) (mean) | a | V % | Length (mm.) (mean) | |
| <i>Aphelenchus modestus</i> | de Man (1884) | 1919 | 30-35 | c 75 | 0.64 | — |
| <i>Aphelenchoides parietinus</i> | Goodey 1951 | 0.6-0.9 | 28-38 | 70 | 0.57-0.75 | 25-30 |
| <i>Aphelenchus parietinus</i> | Bastian 1865 | 0.706 | 23 | 67 | — | 12.7 |
| <i>Aphelenchoides kukuii</i> | Fischer 1894 | 0.61-0.80 (0.7) | 32 | 70 | 0.5-0.62 (0.6) | 14 |
| <i>Aphelenchus microlaimus</i> | Cobb 1893 | 0.7 | 45 | 69 | 0.66 | 42 |
| <i>Aphelenchus ormerodii</i> | Ritzema Bos 1891 | 0.65 | 27 | 66 | 0.61 & 0.55 | 26 & 23 |
| <i>Aphelenchus parietinus</i> | Micoletzky 1922 | 0.35-1.05 (0.62) | 23-43 (31.6) | 70 | 0.35-0.9 (0.605) | 25-47 (34.3) |
| <i>Aphelenchus pyri</i> | Bastian 1865 | 0.59 | 29 | 66 | as ♀ | — |
| <i>Aphelenchus villosus</i> | Bastian 1865 | 0.50 | 20 | 66 | 0.39 | 15 |
| <i>Aphelenchus minor</i> | Cobb 1893 | 0.48 | 34 | 68 | — | — |
| <i>Aphelenchoides parietinus</i> | M.T.F. 1955 | 0.43-0.53 (0.47) | 22-28 (26) | 67 | — | 11-13 (11.75) |

Length

a = —
Greatest breadth

V = Distance of vulva from anterior end as percentage of total length.

TABLE II.

Comparison of differential characters in *A. parietinus* and several related species.

| | Length mm. | a | Tail tip | Stylet | Post vulval sac | Position of vulva V% |
|---|---------------|-------|----------------------|-------------------------|--------------------------------|----------------------------|
| <i>A. parietinus</i> (Bastian, 1865) Steiner, 1932 | 0.43-0.53 | 22-28 | Simple mucro | Basal thickenings | P.v.s. 2-3 body-widths long | 66-70 |
| <i>A. fragariae</i> (Ritzema Bos, 1891) Christie, 1932 | 0.45-0.8 | 45-60 | Do. | Small knobs | P.v.s. over 2 body-widths | 64-71 |
| <i>A. chamelecephalus</i> (Steiner, 1926) Goodey, 1951 | 0.5-0.7 | 26-32 | Do. | No knobs | No p.v.s. | 75-80 |
| <i>A. pusillus</i> (Thorne, 1929) Goodey, 1951 | 0.3-0.31 | 42 | Do. | Knobs | P.v.s. 3 body-widths | 70 |
| <i>A. helophitus</i> (de Man, 1880) Goodey, 1933 | 0.85-1.3 | 45-52 | Acute, with mucro | Knobs | P.v.s. variable | 70 |
| <i>A. latus</i> Thorne, 1935 | 0.4 | 18 | Acute | Well developed knobs | P.v.s. short | 80 |
| <i>A. coffeae</i> (Zimmermann, 1898) Steiner, 1937 | 0.69-0.88 | 24-36 | Star-shaped mucro | Basal thickenings | P.v.s. 2 body-widths | 62-70 |

evidence be produced, to let the nomenclature rest as it is. When detailed descriptions can be made of nematodes which have hitherto been included in the "parietinus group", they can then be compared with the new conception of *A. parietinus sensu stricto*, and a decision made as to their true status.

Neotype. Slide No. 86/1/6 Nematology Department Collection, Rothamsted.

Paratypes. Slide Nos. 86/1/7-10 Nematology Department Collection, Rothamsted.

Type locality. In *Xanthoria parietina* on walls at Broadmoor, Crowthorne, Berks, England.

Diagnosis. *Aphelenchoides* inhabiting *X. parietina* and probably in other similar situations. With measurements and general description as given above. Only females known. Distinguished from other members of the genus by the length and relative width, the curve of the tail when relaxed by heat and the stylet with basal thickenings.

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On a Technique for Infecting Plants with the Potato Root-eelworm, *Heterodera rostochiensis* Wollenweber

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During the course of an investigation into the influence of various environmental factors on the life-history of the potato root-eelworm it became necessary to restrict the time during which the host plants were subjected to infection by the parasites. It was felt that the technique ultimately found satisfactory might be of interest to others.

It is possible, of course, to add a suspension of larvae to the soil in which the host plant is growing; this technique has often been used and I have found it to give satisfactory results. But, for a number of reasons, it is sometimes more desirable to use cysts as the source of infection. In that case the duration of the period during which the plants are subject to attack can be limited either by transferring the plants to cyst free soil, or by removing the cysts. I have used the former method with some success, growing the plants in perforated waxed card containers sunk in infested soil. In a recent account (Fenwick and Reid, 1958) the plants are lifted from the infested soil and their roots thoroughly washed before they are transferred to cyst free soil. But as these workers are careful to point out, even only 22 days after planting, the root system could not be handled without damage; for some purposes it is questionable whether this can ever be done, for it is impossible to transplant without doing some damage and the damage may well be critical for the problem under investigation; moreover, it may be desirable to infect the plants when they have reached a later stage of growth. On the other hand, the objection to a technique in which the cysts are removed is that many larvae may still be present in the soil for a considerable time: the infective time will therefore not be known exactly. It is doubtful however, whether, in the presence of an active growing potato plant, any larvae which are going to enter the plant will lose much time in doing so; but, in the absence of information, the point must be borne in mind.

A number of different techniques were tried with varying success. The technique described here was found to be far superior to the others; it has now been in use for three years and has given very satisfactory results.

Essentially, the technique consists of enclosing the cysts in a thin, narrow, stainless-steel gauze basket, which is sunk in the soil fairly close to the growing plant. After a suitable interval, the containers are readily removed and by examination of the contents of all or a sample of the cysts the number of larvae which have emerged can be determined. Comparison with an initial value for similar cysts gives an estimate of the size of the infection to which a particular plant has been subjected.

Apart from its greater simplicity at a critical time, the advantages of the method over larval inoculation are twofold. Firstly, it is possible for the gauze baskets to be added and removed on instruction at points far from one's centre. Secondly, as the worms are stimulated to attack by the plant itself, the size of the infection will presumably be related, in some way, to the growing plant; this may be of some importance although, clearly, the technique will be useless where it is necessary to ensure that each of a number of replicate plants receives the same number of larvae.

The actual baskets were made of 36 mesh (approx. 0.5 mm.) stainless steel, each of a piece of gauze about 10×1.5 cm. This was folded along its length and spot welded at intervals along the side and one end. The process is very easy and, using a dental mechanic's set, it was found possible to make about 30 in little more than half an hour; and they can of course be used repeatedly.

The apertures in the mesh are on the large side so that only large cysts could be used; but although no tests have been carried out with finer mesh, there is little reason for believing that it would not be equally successful.

The cysts used were derived from the roots of potato plants grown the previous season specifically for the purpose. They were passed through a small sieve made of the same gauze as the baskets and only the retained cysts used for the inoculations. Varying numbers of cysts were used in each basket depending on the duration of the inoculation time. They have been used with success both dry, and after a preliminary soaking. In a typical experiment 400 cysts for each basket were soaked for 8 days. Each lot was then mixed with

a "basketful" of dry sand of appropriate particle size, in order to distribute the cysts, and the mixture added to a basket. On this occasion the plants used were grown in a greenhouse in 10-in. pots of sand. They were fully grown when inoculated. A hole of appropriate size was made in the sand with a pencil about an inch from the edge of each pot and at a slight angle inwards; an inoculation basket was added to each. The baskets were buried almost completely;

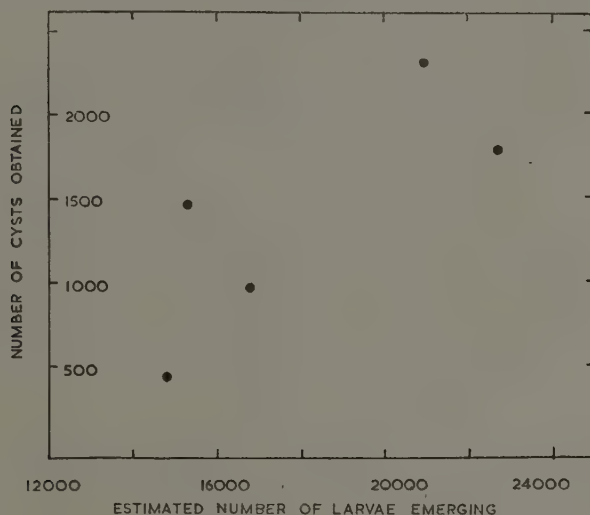


Fig. 1.—Relationship between estimated number of larvae which emerged from inoculation baskets containing 400 cysts and the number of cysts subsequently obtained from the host plants.

but they could be found again quite easily and after 19 days in this particular experiment they were all removed and each was transferred to a test tube so that their identity could be maintained. By examination of the egg contents of a sample of the cysts the total emergence from 400 cysts was estimated. In this particular experiment, the total number of cysts eventually produced by the plants was found later. The results obtained with the method will be published fully elsewhere; but as an indication of its utility, values for total cysts produced are plotted against the estimated infection for five replicate plants in Fig. 1. In the case presented

there is a very obvious relationship between the size of the infection and the ultimate yield of cysts; but, as the technique has enabled me to show, this does not always occur.

This work formed part of a programme supported by grants from the Agricultural Research Council.

SUMMARY.

A description is given of stainless steel gauze baskets used to contain cysts for infecting potato plants.

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The Combined Use of Nematicidal Soil Fumigants and Solubilized Chemicals

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One of the disadvantages of soil fumigants, when used against species of *Heterodera* at such a rate that the parasite is practically eliminated at depths between 2 and 10 inches, is that the kill is unsatisfactory in the surface layer. The ventilation of this layer prevents the accumulation of an adequate concentration of the toxic vapour for a sufficient time.

Rolling the soil, immediately after injection, has been recommended but in field trials has been found of doubtful efficacy (Peters and Fenwick, 1949, p. 376). A light watering of the surface after the injection, to form a temporary seal against the escape of vapours of low water-solubility, might be practicable on a glasshouse scale, but not (in this country) on a field scale; and the same is true of using a gas-tight cover as in methyl bromide injection.

DD MIXTURE.

Some quantitative idea of the magnitude of this problem, and of the effects of light sealing, can be got from a simple experiment in which soil infected with *H. rostochiensis* was injected with Shell DD mixture. The soil was contained in 6 wooden boxes, 6 in. square in plan, and each made up of 8 superimposed sections 2 in. deep. The construction and use of these boxes, to yield data on eelworm densities at various depths, has been described before (Peters, 1953 and 1953a): the only differences on this occasion were (a) that 8 sections were used instead of 6 so that each box contained 20 lb. of soil and was roughly comparable with glazed pots holding the same quantity, and (b) that the boxes were lined with a double thickness of aluminium foil to preclude sorption into the wood; in dismantling the boxes, using a knife as previously described, the foil was readily cut.

Treatments.

In each of the 6 boxes of soil 1 ml. of DD (dissolved in 8 ml. of T.V.O.) was injected 6 in. deep, at a soil temperature of 18°C. and

6% moisture. The boxes were then subjected in pairs to three surface treatments:

- (1) Surface left exposed.
- (2) Surface drenched with about 170 ml. of water.
- (3) Surface covered by laying on it a 7-in. square of aluminium foil, the edges of which were folded against the foil box-linings, but not sealed in any gas-tight manner.

Controls were provided from another experiment, set up on the same day and using the same well-mixed mass of infested soil, in which DD and other fumigants were injected into glazed pots holding 20 lb. of soil. The relevant controls were (in duplicate pairs of pots):

O: Injected with 8 ml. of T.V.O. only.

D: Injected with 1 ml. of DD in 8 ml. of T.V.O. It happened that the surface area of soil exposed in the boxes (36 sq. in.) was about the same as that in the glazed pots (37 sq. in.).

Pots and boxes were left undisturbed, under cover, for 28 days when the soil in the pots was sampled and the boxes were dismantled, all the soil from each layer being separately bagged. By this time the soil had sunk to the bottom of level 1, each box therefore yielding 7 layers or 42 in all.

Cysts were recovered from the soil by floatation and exposed, in duplicate batches of 100, to the hatching stimulus of potato-root diffusate for three weeks at 24°C., following standard procedure. Finally, the numbers of hatched larvae were estimated in a counting slide and expressed as hatched larvae per cyst (l/c). These values were analysed in logarithmic transformation, the presence of some zero counts necessitating the use of: $x = \log (1 + (l/c))$.

Results.

Table 1 shows the "geometric" mean count (l/c) for each level separately and for the entire boxes, under each of the three surface treatments, and for the means of the three, where the percentage kill is also shown.

Since a geometric mean is not calculable for any set of data including a zero, the term is here used for the re-transformed values ($(\text{antilog } x) - 1$) as being more intelligible than logarithms. The analysis of variance (Table 2) shows that there are but slight significant treatment differences, and this is borne out by the values in Table 1.

Sealing, by water or foil, slightly improved the nematocidal effects of DD. These effects were good in levels 4, 5 and 6, significantly poorer in levels 3 and 7, and much poorer again in levels 2 and 8.

TABLE I.

Larvae per cyst (geometric means) at depth-levels after DD injection ;
Mean % kill.

| Level | Larvae per cyst (geometric mean). | | | | | % Kill |
|---|-----------------------------------|------------|-----------|------|--|--------|
| | No. Seal | Water Seal | Foil Seal | Mean | | |
| 2 | 87.7 | 70.8 | 42.2 | 63.9 | | 32.2 |
| 3 | 8.60 | 6.22 | 2.82 | 5.43 | | 93.3 |
| 4 | 0.41 | 0.20 | 0.64 | 0.41 | | 98.5 |
| 5 | 0.62 | 0.45 | 0.64 | 0.57 | | 98.4 |
| 6 | 0.91 | 0 | 0 | 0.24 | | 98.7 |
| 7 | 5.22 | 2.11 | 0.61 | 2.15 | | 96.7 |
| 8 | 53.7 | 37.5 | 25.5 | 37.2 | | 60.2 |
| Whole box | 6.45 | 4.24 | 3.08 | 4.42 | | 95.4 |
| Glazed pots (injected at same rate ; same soil) | | | | 4.58 | | 95.2 |
| Glazed pots (uninjected) | | | | 94.9 | | — |

TABLE II.

Analysis of Variance : $x = \log (1 + 1/c)$.

| Source | | | | | D.F. | Mean Square | Significance |
|------------------------------------|----|----|----|----|------|-------------|--------------|
| Levels (L) | .. | .. | .. | .. | 6 | 2.9879 | $P < 0.1\%$ |
| Treatments (T) | .. | .. | .. | .. | 2 | 0.2405 | $P < 1\%$ |
| L x T ^a | .. | .. | .. | .. | 12 | 0.0301 | (not) |
| Boxes/Treatment (B/T) | .. | .. | .. | .. | 3 | 0.0675 | (not) |
| (L/T) x (B/T) ^b | .. | .. | .. | .. | 18 | 0.0281 | |
| Total | .. | .. | .. | .. | 41 | — | |

^a Error 1, for L, T.

^b Error 2, for (B/T), L x T.

Noteworthy are (a) the close agreement in the overall kill between the control pots D and the boxes, and (b) the marked loss of efficacy at the bottom of each box ; the base was closed by a sheet of perforated zinc and the boxes stood on a flat enamelled surface, nevertheless the escape of DD vapour was considerable : this may also apply to the drainage-tubulure of the glazed pots. In general, a survival rate of about 1.5% (98.5% kill) in levels 4 to 6 was increased to nearly 5%, for the boxes as wholes, by ventilation of the upper and lower surfaces. In the upper 2-in. level of soil, the survival rate was as high as 68% (32% kill). In practice this would go far to waste the good effects of DD.

DD AND CRESOL.

I am indebted to Mr. L. N. Staniland for the suggestion that the surface layer might best be dealt with by drenching with a solubilized nematicide. In 1953 Staniland and Stone showed that many carbon compounds (especially the simpler cyclic compounds), which are of negligible nematocidal effect when applied by ordinary methods, become highly effective when solubilized with a suitable detergent. It was therefore decided to use a 50/50 mixture of *para*- and *meta*-cresols, solubilized in water with Teepol, to drench the surface soil.

Treatments.

The available 48 wooden sections were assembled into 8 boxes of 6 layers (12 in.) deep doubly lined with aluminium foil as before, but this time with a 6-in. square of foil covering the perforated-zinc base. Each box was filled with 15 lb. of sieved, mixed soil infested with *H. rostochiensis*. Since the previous dosage rate of 1 ml. of DD per 20 lb. of soil gave kills rather too high for experimental purposes, half the boxes were injected 14 cm. deep with 0.5 ml. of DD in 10 ml. of acetone and half drenched with 200 ml. of 1% *p-m* cresol solubilized in 0.5% Teepol. Those boxes not injected with DD were injected with 10 ml. of acetone only, and those not drenched with *p-m* cresol were drenched with 200 ml. of 0.5% Teepol only. Thus, the 8 boxes fell, in pairs, under 4 treatments:

O/ Control (Acetone and Teepol only).

D/ DD injection (+Teepol drench).

C/ Cresol drench (+acetone injection).

DC/ DD injection+cresol drench.

Any sealing effect of the drench, and any nematocidal effect of the acetone, were thus kept constant for all boxes. The boxes were treated at a soil temperature of 11°C. and a moisture content of 19%, and were dismantled 28 days later. As before, counts of larvae per cyst, hatching in three weeks at 24°C., were analysed in the transformation $x=(1+(l/c))$.

Results.

The results are summarized in Table 3, which gives the geometric means of larvae per cyst and the per cent. kill, for the three treatments D, C, DC, at each level; the kill was based on comparison with the two

control boxes (O) averaged over all levels. The analysis of variance, in Table 4, shows significant effects, in boxes as wholes, for both DD and cresol, with no significant interaction between them. Levels per treatment (the values of table 3, duly transformed) also differ with high significance leading to the following conclusions:

TABLE III.

Larvae per cyst (geometric means) and % kill at depth-levels after DD, Cresol, and both.

| Treatment Level | DD | | Cresol | | DD + Cresol | |
|-----------------|------------|--------|------------|--------|-------------|--------|
| | <i>l/c</i> | % Kill | <i>l/c</i> | % Kill | <i>l/c</i> | % Kill |
| 1 | 93.2 | 15.7 | 0 | 100 | 1.03 | 98.2 |
| 2 | 70.9 | 35.6 | 43.3 | 60.4 | 16.4 | 84.4 |
| 3 | 7.79 | 92.1 | 76.6 | 30.5 | 2.28 | 97.1 |
| 4 | 0.68 | 98.5 | 92.8 | 16.1 | 0.67 | 98.5 |
| 5 | 3.20 | 96.2 | 96.0 | 13.1 | 1.06 | 98.2 |
| 6 | 12.6 | 87.9 | 121 | 0 | 5.44 | 94.2 |
| Whole Box | 12.4 | 88.0 | 38.5 | 64.6 | 2.71 | 96.7 |

In the control boxes (all levels) mean *l/c* = 111.

TABLE IV.

Analysis of Variance: $\pi = \log(1 + (l/c))$.

| Source | D.F. | Mean Square | Significance |
|--|------|-------------|--------------|
| DD (D) | 1 | 11.4085 | P<0.1% |
| Cresol (C) | 1 | 3.0517 | P<0.1% |
| D x C | 1 | 0.0339 | (not) |
| Boxes/Treatment (B/T) ^a | 4 | 0.0199 | (not) |
| Levels/Treatment (L/T) | 20 | 0.6305 | P<0.1% |
| (B/T) x (L/T) ^b | 20 | 0.0136 | |
| Total | 47 | | |

^a Error 1, for D, C, D x C.

^b Error 2, for (L/T), (B/T).

(a) In the DD boxes, there is no significant difference between levels 1 and 2, but thereafter each of the successive falls to level 4, and rises to level 6, is significant.

(b) In the cresol boxes there is a highly significant rise from level 1 to level 2; the latter is just significantly less than level 6.

(c) In the boxes given both treatments there is a significant rise between levels 1 and 2, and a fall from level 3 to level 4. The rise from level 5 to level 6 is also significant.

From the nature of the apparatus, the objection to standard "analysis of variance" procedure can be raised that, of necessity, the levels cannot be allocated at random. As an additional check, therefore, the mean squares for D, C, and $D \times C$ were calculated for each level separately, using the second error term of the main analysis for comparison. This confirmed that at no level was there any sign of interaction between D and C. It also showed DD to be exerting some effect at level 2 (as well as at levels 3 to 6), and cresol at levels 1, 2 and 3.

It is noteworthy (a) that, in the DD boxes, the use of a square of foil to cover the base greatly reduced but did not eliminate the loss of DD vapour, and (b) that, under the conditions of the experiment, slightly more solubilized cresol might have been used, to deal more effectively with level 2.

SUMMARY AND CONCLUSIONS.

1. The first experiment showed that there is a considerable loss of DD vapour from the surface layer of soil, and that this loss is only moderately reduced by using a water seal or a non-gas-tight seal of foil. The effect of this is to leave a residue of potato root-eelworm "survivors" in the top 2 inches of soil and so to make DD less effective than it would be if the loss could be prevented.

2. The second experiment showed that the survivors could be dealt with by treating the soil surface with a micellar solution of *p-m* cresol, solubilized by the method of Staniland and Stone. It also established the fact that the two treatments behave independently at all levels: there was no interaction between them.

3. The practical implications of this may be of some importance in treating glass-house soils.

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On Some Free-living Marine Nematodes from Kerguelen Island

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AND

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In February, 1953, Dr. Paulian, of Paris, asked the senior author to study his collection of free-living marine Nematodes, collected at Kerguelen Island. The visit of the junior author enabled us to study this material in collaboration; this was the more interesting since she had already made extensive studies of free-living marine Nematodes of the antarctic region (dredged from between 150° E to 40° E by the British Australian and New Zealand Antarctic Research Expedition). Moreover, we had access to the recent monograph of Wieser (1953) on the Enoploidea of Chile.

Although the collection is small, it is composed only of large forms, which even the general zoologist is easily capable of collecting during his exploration and for which no special method is necessary. It does not contain any of the small-sized Chromadoroidea, Araeolaimoidea or other forms, which the helminthologist only finds whilst studying his samples under the binocular microscope. For that reason our material is not very important from an ecological point of view. However, there is definite information regarding the surroundings where the nematodes were observed. Most of these were collected on or near algae, mainly near *Macrocystis*, one of the Laminariaceae, which apparently is very abundant in the Bay of Morbihan. *Macrocystis* is one of the antarctic forms. Another habitat is that of sample 1, of which Dr. Paulian mentions that in the surroundings a great abundance of fixed bivalves were observed together with annelids, crustacea and sponges.

Here we wish to point to the fact that Korringa (1951) in his paper on "the shell of *Ostrea edulis* as a habitat" enumerates under the heading "epizootic Nematodes collected on the exterior of the oyster shell" a number of free-living nematodes, identified for him by Schuurmans Stekhoven (see also Schuurmans Stekhoven, 1942) with *Enoplus communis* Bastian and *Oncholaimus skawensis* Ditlevsen; also present were two species of *Thoracostoma*. All these forms possess a spinneret gland, were all collected from the same habitat and apparently belong to the epifauna of the oyster shells. It is regrettable that Dr. Korringa did not continue his studies on this point. But it is probable that as *Thoracostoma* and related species form the bulk of the present material (no less than 75 of the total of 85 specimens, or 88%), *Thoracostoma* spp. should be considered too as epizoots on bivalves and other sedentary organisms in the tidal region.

LIST OF HABITATS.

All samples in which nematodes were present, viz., in the tubes 1-8, and 11 of the collection, originate from Kerguelen Island, Morbihan Bay. Dr. Paulian gives the following particulars of the habitat concerned to which we add the list of nematodes found in each.

Tube 1.

15th August, 1951, Point Denis (Morbihan Bay) amidst an abundance of fixed bivalves, amongst Annelids, Crustaceans, Sponges, etc.

1. *Thoracostoma antarcticum* (Linstow) 2 ♂♂, 2 ♀♀.
2. *Leptosomatides conisetosum* n.sp. ... 1 ♂.

Tube 2.

1st September, 1951, Pointe Guite (Morbihan Bay), in holdfast of algae, Laminariae, cast on the beach, 40-60 M.

1. *Thoracostoma antarcticum* (Linstow) 1 ♂, 1 ♀.

Tube 3.

25th September, 1951, Morbihan Bay, sand and a variety of algae.

1. *Thoracostoma antarcticum* (Linstow) 2 ♂♂, 3 ♀♀, 1 juv.
2. *Thoracostoma anocellatum* n.sp. ... 1 ♀.
3. *Phanoderma speculum* n.sp. ... 1 ♀.

Tube 4.

25th September, 1951, Morbihan Bay, sand and a variety of algae, 15-20 M.

1. *Thoracostoma campbelli* Ditlevsen ... 1 ♂, 1 ♀, 1 juv.

Tube 5.

16th October, 1951, Morbihan Bay, sand and a variety of algae at the border of a field of *Macrocystis*, Laminariae, 40-50 M.

1. *Thoracostoma anocellatum* n.sp. ... 3 ♂♂.
2. *Thoracostoma antarcticum* (Linstow) 1 ♀.

Tube 6.

21st October, 1951, Morbihan Bay, sand and a variety of algae, at the border of a field of *Macrocystis*, Laminariae, 40-50 M.

1. *Thoracostoma campbelli*, Ditlevsen 4 ♂♂, 5 ♀♀, 6 juv.
2. *Thoracostoma antarcticum* (Linstow) 2 ♂♂.
3. *Thoracostoma anocellatum* n.sp. ... 1 ♂, 1 juv.
4. *Rhabdodemanina calycolaimus* n.sp. 4 ♀♀
5. *Pontonema* sp. ? 1 ♀.

Tube 7.

21st October, 1951, Morbihan Bay (holdfast of *Macrocystis*) at 50 M.

1. *Thoracostoma campbelli* Ditlevsen ... 6 ♂♂, 5 ♀♀.
2. *Thoracostoma antarcticum* (Linstow). 2 ♂♂, 3 ♀♀, 1 juv.
3. *Thoracostoma anocellatum* n.sp. ... 1 ♂, 5 ♀♀.
4. *Rhabdodemanina calycolaimus* n.sp. ... 2 ♂♂.
5. *Phanoderma speculum* n.sp. ... 1 ♀.

Tube 8.

12th March, 1951, Morbihan Bay (holdfast of *Macrocystis*) at 45 M.

1. *Rhabdodemanina calycolaimus* n.sp. ... 1 ♀.

As the foregoing enumerations shows, the composition of the nemic fauna of the different habitats is rather uniform although the numbers of each species varies. All species belong to the Enoploidea.

LIST OF SPECIES.

Family Leptosomatidae.

1. *Thoracostoma antarcticum* (Linstow).
2. *Thoracostoma campbelli* Ditlevsen.
3. *Thoracostoma anocellatum* n.sp.
4. *Leptosomatides conisetosum* n.sp.
5. *Rhabdodemia calycolaimus* n.sp.

Family Phanodermatidae.

6. *Phanoderma speculum* n.sp.

Family Oncholaimidae.

7. *Pontonema* sp.

SYSTEMATICS.

Leptosomatidae.

Thoracostoma Marion, 1870.

1. *Thoracostoma campbelli* Ditlevsen, 1921. (Figs. 1-8).

Campbell Island (Ditlevsen, 1921);

near Punta Arenas Magellans Strait, Chile, Wieser, 1953.

In the present collection this worm was present in tubes 3, 4, 6, 7, 8, all of which were taken in Morbihan Bay, among sand and algae, at depths varying from 15-60 m. A total of 11 males, 12 females, 7 juv. is present. *Thoracostoma campbelli* was described by Ditlevsen from adult males and females, from under stones in the intertidal belt. Wieser described two juveniles from among intertidal algae (58° 11' S, 70° 55' W) in Magellan's Strait near the estuary of the Rio los Ciervos, South of Punta Arenas, in gravel and clay. It has been recognized (P.M.M. unpublished) from Macquarie Island. It thus appears to be a form widespread in the subantarctic regions.

Ditlevsen's measurements:

male L.15.2 mm ; $\alpha=76.8$; $\beta=6.8$; $\gamma=115$.

female L.16.5 mm ; $\alpha=70$; $\beta=6.0$; $\gamma=105$; V.=77%.

Wieser's measurements:

Juv. L. 2.71-5.13 mm ; $\alpha=24.4-33.9$; $\beta=3.7-5.6$; $\gamma=41.6-75.4$.

Kerguelen material, measurements:

m. L. 19.5-19.8 mm; $\alpha=65$.-79; $\beta=6$.1-6.6; $\gamma=100$ -114.

f. L. 16-17.4 mm; $\alpha=51$.6-64; $\beta=8$.0-6.7; $\gamma=84$.2-116; V. 64-66%

Juv. L. 7.9 mm; $\alpha=56$.4; $\beta=4$; $\gamma=87$.7.

It will be seen that in the juveniles the length of the oesophagus and the body width are relatively greater than in the adult, as in most nematodes. The species may be characterized as an *ocellate Thoracostoma* sp. with a deep helmet, the posterior border of which is separated from the remainder of the body by cuticular dots, at least 8 or 4 rows deep; nuchal setae numerous, short, stout, arranged in six rows.

Tail short, blunt, beset in both sexes with numerous fine setae, especially towards the apex. The shape of the gubernaculum is also characteristic, as it bears a small hook near the distal end. Wieser describes and figures the helmet as having only two locules in each lobe; in the present specimens there are sometimes two, but this number may vary, so that there are in some lobes as many as 5 smaller loculi, the number not necessarily constant in all lobes of the same helmet. The constant feature in the specimens from Kerguelen is that the fissures between the lobes are narrow and of some length, ending in a large locule, reaching more than half the distance between the base of the helmet and the lips. The helmet is 50-58 μ . long; the head width at its base 85-90 μ . The granules forming the band, posterior to the helmet are very small and numerous, even in the juvenile specimens, in this point resembling Ditlevsen's figure rather than that of Wieser. The posterior border of the helmet is somewhat crenulated.

An *en face* examination of the head shows clearly the cephalic ring seen by Wieser. However, the "pièce cordiforme" mentioned by him is not present in these specimens. In lateral view there are anterior to the cephalic ring three strongly built chitinous pillar-like structures around the buccal cavity and apparently connected with the helmet. In *en face* view these may be seen to lie more or less at the angles of the trilabiate mouth (see De Man on this in *Th. antarcticum*, 1904, p. 38, Pl. X, 64) and they are the connecting points between the cephalic ring and the helmet. Such a connection between the parts of the buccal skeleton has been noted for the Leptosomatidae by Wieser (1953, 70) and has been seen also in the Enopliidae (P.M.M., unpublished).

The cephalic setae are $\frac{1}{5}$ to $\frac{1}{10}$ of the cephalic diameter; they lie anterior to the mid-length of the helmet. There are 6 small labial papillae.

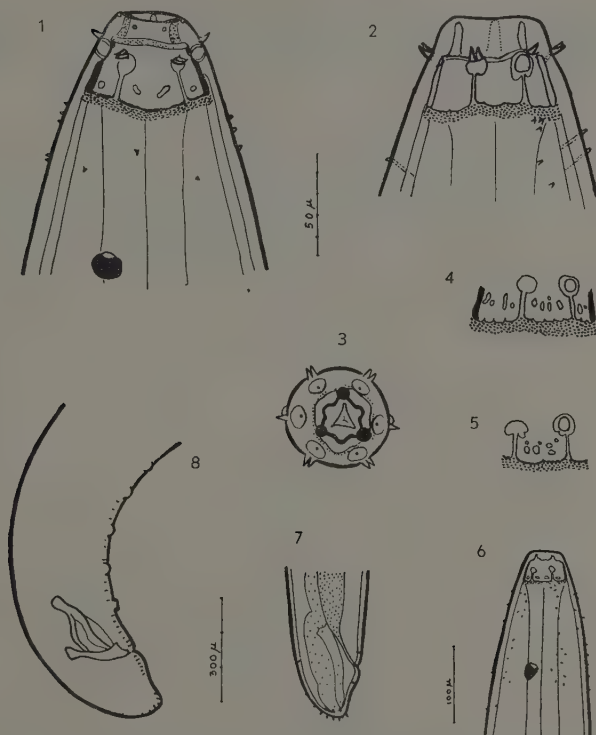
The ocelli are large and lie relatively close to the head at a distance 2.5 to 3 times the length of the helmet (reckoned without the band of granules) from the anterior end. The nerve ring lies at $\frac{1}{3}$ to $\frac{1}{4}$ of the oesophageal length; Wieser and Ditlevsen describe it as at $\frac{1}{3}$ of the oesophageal length.

The tail in both sexes is short, distinctly less than the anal width. It has as mentioned above, numerous scattered setae especially near the tip; these were not figured by Ditlevsen or Wieser. In the male the spicules and gubernaculum, while of the same shape as figured by Ditlevsen, are longer, the spicule being 0.27 mm. and the gubernaculum 0.2-0.19 mm. There are two subventral rows of very small setae extending from posterior to the anus to the first pair of preanal papillae; these were apparently overlooked by Ditlevsen. The preanal papillae number 6 pairs.

The figure of the head given by Ditlevsen does not allow us to conclude with certainty that there is a distinct "pièce cordiforme." Ditlevsen's figure shows at the anterior end 3 pieces, all of which might be called cordiform cuticularisations. These 3 correspond in our interpretation with the three pillar-like strengthenings of the buccal cavity. So we consider our species to be the same as Ditlevsen's. There is reason to doubt that Wieser's 2 juvenile specimens really belong to *T. campbelli*, firstly because of the apparently strongly-developed dorsal cordiform piece, more like that seen in *T. antarcticum* and secondly of the scarcity of cuticular fragments behind the border of the helmet.

There remains the question as to whether Allgén (1951, 334) is correct in synonymizing *T. campbelli* with *T. coronatum* Eberth.

Bresslau and Schuurmans Stekhoven (1940, 14, Pl. III) have carefully compared existing figures and accounts of *T. coronatum* (in that work erroneously synonymized with *T. figuratum* instead of *T. figuratum* with *T. coronatum*). It appears that there are distinct differences between this species and *T. campbelli*. The female tail of *T. coronatum* is distinctly longer and more slender; there are also differences in the shape of the male tail, which is more plump in *T. coronatum*. The cuticular dots posterior to the helmet in *T. coronatum*



Thoracostoma campbelli: 1. Dorsal view of head. 2. Sublateral view of head. 3. End-on view of head. 4, 5. Border of helmet on different specimens. 6. Anterior end. 7. Female tail. 8. Male tail.

(Figs. 1, 2, 3, 4 and 5 to scale beside Fig. 1. Figs. 7 and 8 to scale beside fig. 8.)

are fewer and larger than in *T. campbelli* and appear in part to overlie the helmet.

It is probable that more spp. than are at present known are in possession of such cuticular granules and that to this group belong: *T. coronatum*, *T. campbelli* (in which they are most pronounced) and the specimens studied by Wieser.

We trust that further studies will be made of Wieser's specimens, especially of the top view of the head, so that it may be ascertained if there is only one "cordiform" dorsal tooth or three pillar-like structures.

Thoracostoma anocellatum n.sp. (Figs. 9-12).

In spite of the absence of lenses or pigment spots this Thoracostome is not placed in the subgenus *Pseudocella*, as the spicular apparatus shows that its affinities lie with *Thoracostoma* s.str. The species is present in tube 1 from Pointe Denis, Morbihan Bay (among bivalves and other intertidal forms) and in tubes 3, 5, 6, 7 and 8 from the Morbihan Bay (among sand and algae at depths from 15-60 m.) a total of 11 ♂♂, 16 ♀♀, 2 juv. It has also been recognized (P.M.M. unpublished) from various depths along the Antarctic Coast.

Dimensions, Morbihan Bay:

male L.21.8-23.1 mm ; $\alpha=84-96.2$;
 $\beta=6.4-6.6$; $\gamma=135-145$.
female L.23.5-27.9 mm ; $\alpha=73.4-93$;
 $\beta=6.2-8.3$; $\gamma=117-140$; V.=55.3-59.1%.

Dimensions, Antarctic (P.M.M.):

male L.13-18 mm ; $\alpha=48-49$; $\beta=4.8-6$; $\gamma=82-106$;
female L.12-17 mm ; $\alpha=38-42$;
 $\beta=5.1-5.7$; $\gamma=84-87$; V.=55-64%.

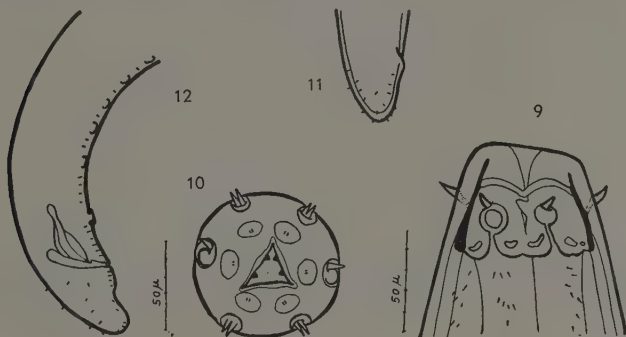
The species may be distinguished as an anocellate Thoracostome, with medium sized helmet, with main locules at its midlength, setiferous cuticle, head truncated obliquely and gubernaculum without lateral anterior projections. The measurements given above show that the Kerguelen specimens are much larger than the Antarctic, but the resemblance is however so great that there can be no question of there being two species.

The cuticle in nuchal and caudal regions bears a number of setae, longer and finer than in other species of the genus described here.

The head is obliquely truncated, sloping towards the dorsal side ; the dorsal lobe of the helmet is distinctly shorter than the ventral, the lateral lobe of a length between these two. The borders of the lobes are curved and indented ; the fissures between the lobes are relatively narrow but short, and the wide locules into which they

open are posterior to the mid-length of the helmet. There are generally two but there may be more or fewer loculi in each lobe. The length of the helmet (lateral) is $48-53\ \mu$, the width of the head at its base is $80\ \mu$.

The cephalic setae are about $\frac{1}{4}$ to $\frac{1}{8}$ of the cephalic diameter. In *en face* view it is seen that there are two small teeth on the rim of the two subventral lips, but none on the dorsal lip; the latter is strongly cuticularized along its whole length, presumably forming a cutting plate. The nerve ring is about a quarter of the length of the oesophagus from the anterior end.



Figs. 9-12. *Thoracostoma anocellatum* n.sp.

9. Sublateral view of head. 10. End-on view of head. 11. Female tail. 12. Male tail.

The female tail is 0.2 mm. long, a little more than the anal breadth. The eggs vary in size in different females, from $86-180\ \mu$ in length by $220-250\ \mu$ wide.

The male tail is 0.15-0.17 mm. long, a little shorter than the anal breadth. The spicules are 0.23 mm. long, with the median flexure characteristic of the subgenus and a lateral flange. The gubernacula are 0.15-0.17 mm. long without an antero-lateral projection but with a small beak towards the distal end. A row of setae extends on each side of the ventral line from just behind the anus to the level of the anteriormost of the 6-8 preanal papillae; the setae are closest together in the adanal region, becoming fewer more anteriorly. The median preanal organ lies a little less than the tail length in front of the anus. The tail in both sexes bears a rather large number of slender scattered setae, especially numerous near the tip.

Thoracostoma antarcticum (Linstow, 1891) (Figs. 18-19).

Syn. *Leplosomatium antarcticum* Linstow, 1891.

Thoracostoma antarcticum, Linstow, 1902.

Thoracostoma polare Cobb, 1914.

Thoracostoma antarcticum so far recorded from the American sub-antarctic zone (St. Georgia, among algae, sponges and ascidians; Cape Adare; Navarrin Island, Puerto Toro, tidal beach; Tierra del Feugo, Torrent Bay, Londonderry Island, French Canal; Ross Sea), is now recorded at Kerguelen Island. *T. polare* Cobb, 1914, from Cape Roys in the Ross Sea is now considered a synonym. The shape of the helmet figured by him and his measurements are within the variations possible for the species, although he does not describe the gubernacular extensions seen by other authors.

T. antarcticum has also recently been recorded from other parts of the Antarctic Ocean by Mawson (unpublished P.M.M.).

In the present collection (10 ♂♂, 10 ♀♀, 2 juv.) it is present in tubes 2, 3, 5, 6, 7, 8 from the Morbihan Bay, either among *Laminaria* holdfasts cast on to the beach, or from sand and weeds at depths from 15-60 m.

Dimensions, Morbihan Bay:

♂ L.=18-19.5 mm.; α =65-74.4; β =6.2-6.5; γ =97-97.5.

♀ L.=15.8-20.9 mm.; α =52.8-68;

β =5.7-5.9; γ =68.1-87.7; V.=63.1-63.3%.

Dimensions, Antarctic (P.M.M.).

♂ L.13-18 mm.; α =42-51; β =5.3-6.3; γ =102-185.

♀ L.13-18 mm.; α =40-56; β =5.2-6.1; γ =96-117; V.60-67%.

Dimensions by De Man, re-examining Linstow's original specimens:

♂ L. to 17.3 mm.; α =60-70; β =5.75; γ =125-150.

♀ L. to 19.5 mm.; α =60-70;

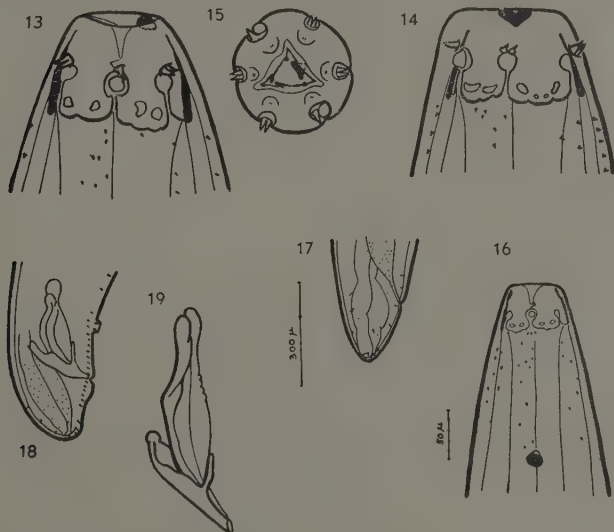
β =6.5-6.25; γ =125-147; V.=62-67.6%

Dimensions by Cobb:

♂ L. 19 mm.; α =66.6; β =8.3; γ =166.

♀ L. 19.3 mm.; α =66.6; β =7.1; γ =388; V.60%.

A very full description of this species is given by De Man (1904) and the specimens from Kerguelen agree with his description and figures, except in the point of exact values for α , β and γ . The head is truncated in a very slightly oblique direction, so that the helmet is a very little longer on the ventral side; this condition is much less marked than in *T. anocellatum*, and was not commented on by De Man. The helmet border is not greatly lobed, generally appearing



Figs. 13-19. *Thoracostoma antarcticum*.

13, 14 and 15 lateral, dorsal and end-on views of head. 16. Anterior end.

17. Female tail. 18. Male tail. 19. Spicula and gubernaculum.

(Figs. 9, 13 and 14 to scale beside fig. 9. Figs. 10 and 15 to scale beside fig. 10. Figs. 11, 12, 17 and 18 to scale beside fig. 17. Figs. 16 and 19 to scale beside fig. 16).

under low power as an almost straight line across the head. The clefts between the lobes are long and narrow, but in many cases less so than figured by De Man. The lateral clefts are shorter than the others, and the lateral lacunae in which the amphids lie, are correspondingly longer. The lacunae within the lobes are generally two, situated near the border of the lobe, but in some there are more than two.

The cephalic setae are short and conical and are $\frac{1}{8}$ to $\frac{1}{10}$ of the cephalic diameter in length. The lips bear teeth as figured by De Man, two small ones on each of the sublateral lips and a very large bipartite tooth ("pièce cordiforme") on the dorsal, the latter structure being very striking in *en face* and side views of the head. A dorsal tooth is present in the buccal cavity.

Nuchal setae are present, although they are as mentioned by De Man, rather small. The ocelli are $\frac{1}{8.5} - \frac{1}{4.5}$ of the distance from the anterior end to the nerve ring and the latter is $\frac{1}{3.5} - \frac{1}{4}$ of the length of the oesophagus.

The female tail is about equal in length to the anal breadth. It is rounded at the tip and bears scattered small setae. The male tail is rather shorter than the anal breadth, and in addition to the adanal setae bears small setae near the tip and a few others between the level of the anus and the tip.

The spicules are 0.2–0.22 mm. long, with a double head. The gubernaculum is 0.19 mm., and bears a narrow anteriorly directed lateral projection, as figured and described by De Man. There are usually six pairs of preanal papillae, though the anterior one or two of these may be very small. A row of small setae extends from just behind the anus to the level of the posterior—most preanal papillae, and one or two may lie between the successive papillae. The preanal organ is at about the level of the midlength of the spicules, or a little less than the length of the tail in front of the anus.

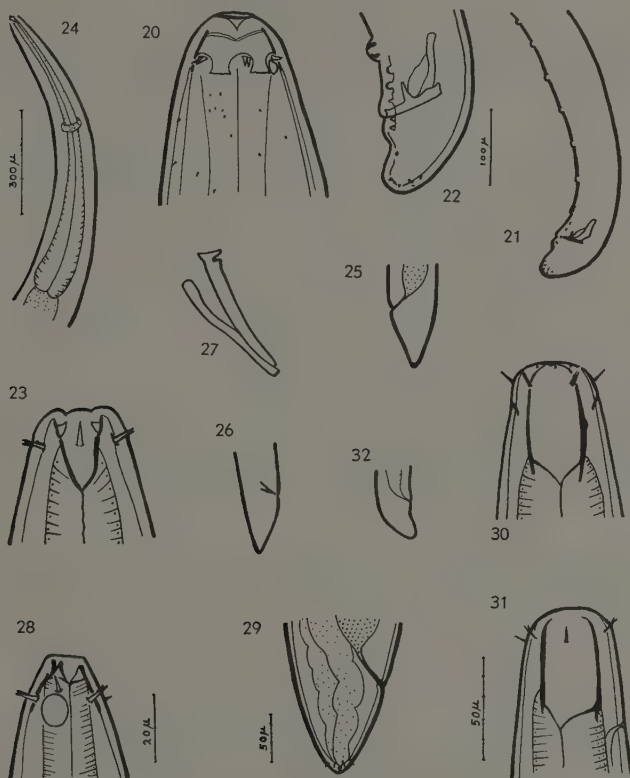
Leptosomatides Filipjev, 1918.

Leptosomatides conisetosum n.sp. (Figs. 20–22).

A single male worm of a new species was present in tube 1, from among bivalves and algae at Point Denis.

L. 12 mm.; $\alpha=80$; $\beta=6.6$; $\gamma=120$.

The setae in the nuchal and caudal region are short and conical, and not very numerous. The helmet is well developed, but not so strongly cuticularized as in species of *Thoracostoma*, so that the posterior border is not so obvious under the low power. It is 25μ in length and the body width at its posterior border is 55μ . The lobes are short with straight edges posteriorly; the spaces between the lobes are almost semicircular.



Figs. 20-22. *Leptosomatides conisetosum* n.sp.

20. Dorsal view of head. 21. Posterior end of male. 22. Tail of male.

Figs. 23-27. *Rhabdodemanina calycolaimus* n.sp.

23. Head. 24. Oesophageal region. 25. Tail of female. 26. Tail of male.

27. Spicula and gubernaculum.

Figs. 28-29. *Phanoderma speculum* n.sp.

28. Head, lateral view. 29. Tail.

Figs. 30-32. *Pontonema* ? sp.

30 and 31 lateral and ventral views of head. 32. Tail.

(Figs. 20, 27, 30 and 31 to scale beside fig. 31.

Figs. 21, 24, 26, 32 to scale beside fig. 24.

Figs. 23 and 28 to scale beside fig. 28).

The 10 cephalic setae, about $\frac{1}{3}$ of the cephalic diameter are near the posterior edge of the helmet; the amphid lies so that its anterior part only is within the helmet area. The diameter is $\frac{1}{8}$ of the corresponding body width.

Eyes with lenses are present, 0.1 mm. from the anterior end. The nerve ring surrounds the oesophagus at the end of its first quarter.

The male tail is of the form typical in this genus; the preanal organ lies at the level of the proximal end of the spicule, there are eight pairs of preanal papillae, each associated with a seta, in front of the preanal organ, and two more pairs, much smaller between the preanal organ and the anus; in addition there are about 4 pairs of small adanal setae, as well as more setae, scattered near the tip of the tail.

The spicule is 0.13 mm. long; the gubernaculum is 0.92 mm. long, and has an anteriorly directed lateral spine, reaching to the flange of the spicule. The length of the tail is 0.1 mm., the anal breadth is 0.11 mm.

The species differs from *Thoracostoma* species in the shape of the helmet. In this feature it resembles *Synonchus* sp. from the Mediterranean region.

It was recognized in southern collections from the antarctic ocean (P. M. Mawson, in course of publication).

The species is very close to *L. euxina* Filipjev, but is distinguished by the rather long helmet, the more forward position of the ocelli and by the longer, and equal, spicules, the longer gubernaculum and the more numerous preanal papillae.

Rhabdodemia Baylis and Daubney, 1926.

Rhabdodemia calycolaimus n.sp.

Figs. 23-27.

Five females and two male worms of a new species of the genus *Rhabdodemia* were taken from tubes 6, 7 and 11, all from Morbihan Bay, at a depth of 40-50 m.

♂, L. 6-7.5 mm.; $\alpha=31.5-37.5$; $\beta=7.1-7.8$; $\gamma=33.3-37.5$.

♀, L. 6.2-6.8 mm.; $\alpha=32-34$;

$\beta=6.4-7.5$; $\gamma=34.4-44.4$; V.55-60.9%.

The cephalic setae, about $7\ \mu$ long, $\frac{1}{4}$ of the cephalic diameter, are arranged in a single circle of 10 setae, at a distance of $10\text{--}12\ \mu$ from the anterior end. The labial papillae are extremely small. The amphids were not seen. The buccal capsule is composed of two parts, the anterior being cylindrical and the posterior funnel-shaped. The anterior is $60\ \mu$ long, $12\ \mu$ in diameter and from its walls project 3 small teeth. The posterior part is $15\ \mu$ long. By analogy with other species of *Rhabdodemania* there should be three ridges on the walls of this part, ending in tooth-like projections. These if present, are very faint. The oesophagus widens gradually in its hinder third, the nerve ring surrounds it at a little anterior to its midlength. The tail in both sexes is conical. In the female it is $0.15\text{--}0.18$ mm. long, in the male $0.18\text{--}0.20$ mm. and the anal breadth is $0.1\text{--}0.11$ mm. in the female and 0.1 mm. in the male. The tip is blunt. The eggs are $0.2\text{--}0.8$ mm. long, $0.12\text{--}0.15$ mm. wide. The spicule is $65\text{--}75\ \mu$ long, with enlarged head, separated from the rest by a constriction; the gubernaculum is $63\text{--}70\ \mu$ long, rod-shaped and slightly bent at its middle. No accessory papillae were seen.

The species is closest to *R. laticauda* (Ditlevsen, 1926). It differs from it in the size of the gubernaculum, in relation to that of the spicule, and in the absence (or small size) of the teeth in the posterior part of the buccal cavity.

Phanodermatidae.

Phanoderma Bastian, 1865.

Phanoderma (Alyncoides) speculum n.sp. (Figs. 28–29).

Two young ♀♀ of a new species of *Phanoderma* were present in the tubes 8 and 7.

L. ♀ $6.4\text{--}6.2$ mm.; $\alpha=54.5\text{--}81$; $\beta=5\text{--}4.5$; $\gamma=75\text{--}62$; V. $61.7\text{--}63.7\%$.

There are six cephalic setae, the submedian ones about a third of the cephalic diameter, the lateral ones rather shorter. The helmet was seen only in profile. It is $16\ \mu$ deep, and the body width at its base is $25\ \mu$. The cephalic setae are just anterior to the border of the helmet. The amphid is outstandingly large, its diameter $\frac{2}{3}$ of the corresponding head diameter. Four rather long fine nuchal setae are present, in submedian positions. The ventral gland is post-oesophageal, the position of the excretory pore is not certain, but is probably twice the helmet width from the head. The nerve ring is at $\frac{1}{3\frac{1}{2}}$ of the oesophageal length from the head. Eyes are absent.

In the 6.2 specimen the flexure of the anterior ovary is 0.65 mm. and of the posterior 0.55 mm. from the vulva. In the shorter specimen two eggs are present, measuring 330 by 90 μ .

The tail is a very little longer than the anal breadth; it is conical and rounded at the tip where it bears a ring of about 6 short setae. The caudal glands are preanal.

There are two short-tailed anocellate species of *Phanoderma*, *P. islandicum* Ditlevsen, 1926, and *P. pacificum* Wieser, 1953. The present specimens differ from the former in having shorter cephalic setae and a shorter tail and from the latter in the size of the amphid, the relative length of the helmet and in the position of the excretory pore which is not so far forward as in Wieser's species.

Oncholaimidae.

Pontonema Leidy, 1855.

Pontonema (?) species (Figs. 30-32).

One ♀ Oncholaimid worm was present in tube 6 from sand and algae from 40-50 m., in Morbihan Bay. The buccal capsule is filled with grit, and it is impossible to be sure of the position or even the presence of teeth.

L. ♀ 13.5 mm.; $\alpha=112.5$; $\beta=8.4$; $\gamma=135$; V. 63.7%.

The body is long and thin and coiled in double spiral. Some few scattered setae, very small, are present in the nuchal region. There are 10 cephalic bristles, each $\frac{1}{4}$ of the cephalic diameter, in a ring 10 μ from the anterior end. The amphids, which are very small, are 10 μ behind the setae, just in front of the middle of the buccal cavity. The excretory pore is 60 μ from the anterior end, just posterior to the buccal capsule. Lips and small labial papillae are present. The buccal capsule is 52 μ long, 25 μ wide and its length is $\frac{1}{3}$ of the length of the oesophagus. A large triangular yellow structure lies in the capsule at the level of the cephalic setae, but it could not be ascertained if this were a tooth or a small sand grain. No other teeth could be seen, owing to the sand in the buccal capsule. Eggs are 0.17-0.2 by 0.1 mm. The tail is 100 μ long, conical with rounded tip. The anal width is 80 μ .

The possible presence of one tooth suggests the genus *Mononcholaimus*. However, the size of the body and the shape of the tail is unlike most species of the genus. Moreover, *M. longidentatus*

Stekhoven, in which the tail is shorter, has very large amphids, while those of the present specimen are very small.

The body form and size suggest a species of the Genus *Pontonema*. As some specimens of this genus have been seen in which the three teeth are very lightly chitinated, (Mawson, not yet published) it is thought that they may in this specimen be concealed by the grit. If it belongs to this genus it would fall closest to *P. hackingi* Mawson, 1952, with which it agrees in the shape of the buccal cavity, the position and size of cephalic setae, amphids and excretory pore and in the shape of the tail. It differs from it in the α and γ values and the vulva is rather further back than in *P. hackingi*.

(In a recent letter from Adelaide, P.M.M. states she has found more specimens of the same species, which proved to belong to the genus *Pontonema*, as suggested above).

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The Genera and Species of the Subfamily Rhabditinae Micoletzky, 1922 (Nematoda): a Nomenclatorial Analysis—including an Addendum on the Composition of the Family Rhabditidae Örley, 1880*

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Osche (1952) has recently published a sorely needed, comprehensive revision of the genus *Rhabditis* Dujardin [1844] (*sensu lato*) including detailed study of certain features of the cephalic end, especially of the stoma or mouth cavity. For some time to come his study will surely be the point of departure for morphological and systematic work on the group. On the basis principally of the structure of the metastom (a subdivision of the stoma) and of the esophagus, he recognizes some eight subgenera in the genus *Rhabditis*, which are as follows: *Rhabditis* Dujardin [1844] (*sensu stricto*), *Choriorhabditis* Osche, 1952, *Telorhabditis* Osche, 1952, *Caenorhabditis* Osche, 1952, *Mesorhabditis* Osche, 1952, *Teratorhabditis* Osche, 1952, *Protorhabditis* Osche, 1952, and *Parasitorhabditis* Fuchs, 1937. For all of these save the last he lists the species recognized by him. For a revision of *Parasitorhabditis* he refers to an unpublished manuscript by Rühm.

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In a recent brief paper (Dougherty, 1959) I have undertaken to raise Osche's subgenera to the rank of genus and have recognized subgenera for the "species-groups" into which he divides his largest two subgenera, *Rhabditis* and *Choriorhabditis*. However, I have not therein attempted to justify these actions, nor to explain my choice of names. In a group as important as the Rhabditinae, adequate documentation of nomenclatorial revision is much needed. It was initially my feeling that this revision would best be done by Dr. Osche, with whom I have been in friendly communication. However, he is not in agreement with the elevation of most of his subgenera to generic status. He has therefore left the task to me.

A critique of Osche's system is here undertaken for two reasons. First, his classification is over-conservative; the criteria on the basis of which he has established his subgenera amply justify full generic status for the groups of species in question. (One need but compare the trivial bases on which many workers on parasitic nematodes erect genera to appreciate Osche's laudable, but over-caution!) Second, he has not followed the International Rules of Zoölogical Nomenclature in his selection of names for certain of his subgenera and in a number of other instances; certain changes have consequently been necessary (Dougherty, 1959). He has overlooked a few names that apply to species in the *Rhabditis*-group, and, as for those listed by him as synonyms of the genus *Rhabditis*, he has in most cases made no evaluation of them. Certain of these names are earlier synonyms of his subgeneric names; others apply to species that fall outside the *Rhabditis*-group (i.e., outside the subgenera recognized by Osche) or even outside the family Rhabditidae Örley, 1880.

The various names that have been, should be, or might be applied to the genus *Rhabditis* (*sensu lato*) are here reviewed and, where possible, their disposition in accordance with the International Rules of Zoölogical Nomenclature is explained. The genera, subgenera, and species that I would accept in the sub-family Rhabditinae Micoletzky, 1922, are listed. The present paper is intended primarily as a contribution to the nomenclature rather than the taxonomy of the subfamily. Other than the change in taxonomic status of Osche's subgenera most of the problems treated here are nomenclatorial ones. I have in a number of cases, however, found it necessary or desirable to pass new judgment on the taxonomic status of certain genera, subgenera, and species, particularly where a vital nomenclatorial question is involved. (Moreover, see ADDENDA for more comprehensive taxonomic decisions.)

I. A REVIEW OF THE GENUS *Rhabditis* (*sensu lato*).

Whether Osche's eight taxonomic units are left as subgenera or raised to generic rank, the correct names to be applied to them must be established. He lists some nine names as falling as total synonyms of *Rhabditis*, thereby implying that their type species are congeneric with the type species of *Rhabditis*; in this he follows many previous workers (such as Goodey, 1951). These names are: *Tribactis* Dujardin [1844]; *Leptodera* Dujardin [1844] (incorrectly assigned to Schneider (1866) by Osche); *Ascaroides* Barthélemy, 1858; *Pelodytes* Schneider, 1859; *Pelodera* Schneider, 1866; *Diploscapteroides* Rahm, 1928 (incorrectly dated "1930" by Osche); *Rhabditoides* Goodey, 1929; *Rhabditella* Cobb, 1929 (subgenus, raised to genus by Chitwood (1933a)); and *Cuticularia* van der Linde, 1938. In addition to the foregoing names the following, not considered by Osche, should be evaluated: *Leptoderes* Dujardin [1844]; *Leptodora* Dewitz, 1892; *Cruznema* Artigas, 1927; *Cephaloboides* Rahm, 1928 (established as a subgenus and assigned to the genus *Rhabditis* by its author); *Pseudorhabditis* Kreis, 1929; *Asymmetricus* Kreis, 1930; *Agfa* Chitwood, 1935; and *Epimenides* Gutiérrez, 1949.

These names, plus *Rhabditis* Dujardin [1844] and *Parasitorhabditis* Fuchs, 1937 (one of Osche's subgenera) are herein considered in chronological order, and their status determined where possible.

1. *Rhabditis* Dujardin [1844].

This genus was established by Dujardin (1844, pp. 239-243) for four species, without designation or indication of type—*R. terricola* Dujardin [1844], *R. aceti* (= *Vibrio aceti* Müller, 1783), *R. tritici* (= *Vibrio tritici* Steinbuch, 1799), and *R. glutinis* (= *Vibrio glutinis* Müller, 1788). Stiles and Hassall (1905, p. 46) held that Bastian (1865) selected *R. terricola* as type of *Rhabditis*. However, I feel that this contention is untenable, for Bastian (p. 129) merely referred to "the typical *Rhabditis terricola*" and in his paper gave no evidence of recognizing the concept of types. Article 30, rule (g), of The International Rules of Zoölogical Nomenclature states that "the expression 'select the type' is to be rigidly construed" and that "mention of a species as an illustration or example of a genus does not constitute selection of a type." However, Stiles and Hassall may themselves be considered to have selected the type in stating, even

though erroneously, that Bastian did so; at Paris in 1948 the International Commission (1952, *Bull. Zool. Nomencl.*, vol. 4, pp. 181-182) decided that an author selects a type species if he "does no more than state that a specified such species is the type species of the nominal genus concerned, irrespective . . . of whether he states or implies, either correctly or otherwise, that the nominal species has been selected by some previous author to be the type species of that nominal genus. . ." As Stiles and Hassall were first to fix a species as type of *Rhabditis*, their selection must stand. (Later in their paper (p. 134) they alternatively suggested *Vibrio glutinis* as type, but this selection may be dismissed, for that of *R. terricola* has page priority, and no subsequent worker has accepted *V. glutinis* as type.) The remaining three species originally put in *Rhabditis* by Dujardin are not rhabditids; they were removed to other genera by subsequent investigators and today are correctly known as *Turbatrix aceti* (Müller, 1783) Peters, 1927 [family Cephalobidae], *Anguina tritici* (Steinbuch, 1799) Chitwood, 1935¹ [order Tylenchida], and *Panagrellus redivivus* (Linné, 1767) Goodey, 1945 [family Cephalobidae], respectively.

The genus *Rhabditis* Dujardin, 1845 [sic], has already been placed on the *Official List of Generic Names in Zoölogy* by action of the International Commission on Zoölogical Nomenclature in Opinion 104 (1928); the type species there accepted was "*terricola*" (type "by subsequent designation (1865)" [= "selection" by current terminology—see 1950, *Bull. zool. Nomencl.*, vol. 4, p. 179]. Thus this genus has come into the most official of status.

It is obvious that, as type of the genus *Rhabditis*, the nominal species *R. terricola* is very important, and an effort must be made to identify it in a satisfactory manner with a taxonomic species. Otherwise the nomenclature of the large group of species in the broad genus *Rhabditis* cannot be stabilized without an appeal to the International Commission on Zoölogical Nomenclature. It is therefore unfortunate that, despite our much advanced knowledge of the rhabditids, the identity of *R. terricola* admittedly cannot be determined beyond question from the description given by Dujardin. It is obvious from his discussion, following the description proper, that he included in his concept of *R. terricola* a number of different species, some variously parasitic in fish, amphibians, snails, and earthworms. Nevertheless, with the orientation of Osche's organization of species within the broad genus

¹ 1935a.

Rhabditis, the description itself, which must have been made from a free-living culture, permits one to delimit rather well the group of species to which the name may reasonably be applied.

Örley (1885, 1886) and a number of subsequent workers, for example, Railliet (1893, p. 550) and Chitwood (1933c), have chosen to sink *Pelodera teres* Schneider, 1866—which was well described in the original—as a synonym of *R. terricola*, thus restricting the nominal species *R. terricola* to the taxonomic species rather widely known as *R. teres* [(Schneider, 1866), Butschli, 1873], in continental Europe. But others, such as Micoletzky (1922), have regarded *R. terricola* as a *species inquirenda* and have taken the nominal species *Pelodera teres* as type of *Rhabditis*. This is, of course, quite inadmissible under the International Rules. As Chitwood (1933c) pointed out, to make *R. terricola* a *species inquirenda* automatically makes *Rhabditis* a *genus inquirendum*; in no case short of action in which plenary powers are invoked by the International Commission can the nominal species *P. teres* be taken as type of *Rhabditis*.

Only Reiter (1928) has adequately taken issue with the synonymizing of *R. terricola* and *P. teres*, pointing out that characters and measurements given by Dujardin preclude identifying the two nominal species as one and the same taxonomic species. Chitwood himself admitted that certain data of Dujardin (namely the number of papillary pairs in the male bursa) are in conflict with such an identification, but in effect argued that all disagreements could be attributed to the inaccuracies of early helminthological descriptions.

I have checked this question carefully and find myself forced to agree with Reiter. *P. teres* cannot be reasonably construed as fitting the detailed part of the original description of *R. terricola* even with generous allowance made for errors of observation on Dujardin's part. There is no evidence, moreover, that *P. teres* was included in the admittedly diverse group of species referred to *R. terricola*, but not specifically described by Dujardin. His completely described free-living form was relatively large (up to 1.05 mm. in the male and 2 mm. in the female), the male having a short leptoderan posterior end,² supplied with a clearly defined bursa bearing 7 to 8 papillae,³ and the

² " . . . queue courte, un peu courbée, terminée en pointe fine . . . "

³ " . . . munie en dessous de deux ailes latérales, soutenues par sept à huit côtes chacune . . . "

female having a long, slender tail⁴ and an approximately median vulva with amphidelphic gonads.

The foregoing points clearly eliminate not only *P. teres*, but all the species placed by Osche in his subgenus *Rhabditis*, which are characterized by peloderan bursae and generally short, conical or dome-shaped female tails. On the other hand the enumerated characters agree well with, and only with, those of the species placed by Osche in the "*maupasi*-group" of his subgenus *Choriorhabditis*; they disagree in certain vital points with the characters of Osche's other species-group of this subgenus. It therefore must be concluded that the identity of the free-living forms described under the name *R. terricola* has to lie with the species placed by Osche in his "*maupasi*-group." Of these species, agreement with the description of *Rhabditis aspera* Bütschli, 1873, as given by Reiter (1928), is striking—not only in qualitative features, but in the few measurements given by Dujardin (maximum body length, length of spicules, length of female tail). It is true that *R. aspera* has 9 papillary pairs in the male, but here the accuracy of Dujardin's observation may indeed be questioned; he could easily have overlooked the anteriormost pair, which are small and inconspicuous.

No doubt it cannot be stated with absolute certainty that *R. aspera* and *R. terricola* (*sensu stricto*) are one and the same species; the former, as it is generally understood today, appears to be the most common of a group of morphologically closely related species, including—aside from *R. aspera*—*R. lucianii* Maupas, 1919, *R. gongyloides* Reiter, 1928, etc. However, nothing in the detailed part of the original description of *R. terricola* precludes its application to *R. aspera*, and agreement is best with this species of all known in the group.

I therefore feel that, in view of the untenability of synonymizing *Pelodera teres* with *R. terricola* and at the same time in view of the desirability of conserving the nominal genus *Rhabditis* without recourse to the International Commission on Zoölogical Nomenclature, the logical and reasonable thing to do is to restrict the name *R. terricola* to the taxonomic species now generally known as *R. aspera*, as I have already done without explanation (Dougherty, 1953). Inasmuch as the genus *Rhabditis* (*sensu lato*), taken *in toto* for the first time, has

⁴ "... queue droite, amincie et prolongée en pointe fine plus au moins longue: —anus à 0mm.,14 au moins de l'extrémité . . ."

only just been fragmented into genera, the shift of type from the taxonomic species commonly known as *R. teres* to that commonly known as *R. aspera* should not work a hardship. Moreover, the consequent suppression of the specific name *aspera* does not involve a species with a significant popular or applied scientific literature. The new application of the specific name *terricola* inevitably will involve some initial confusion, but the reestablishment of the specific name *teres* has compensating virtue, for in Europe this name is widely used instead of *terricola*. In view of the fact that no previous taxonomically defensible restriction of the name *terricola* has been made, its application to the taxonomic species generally known as *R. aspera* should be legally binding for nomenclatorial purposes.

The consequence of the foregoing act is to shift the generic name *Rhabditis* from the taxonomic genus based on Osche's subgenus *Rhabditis* to that based on his *Choriorhabditis*. The latter name thus falls, at the generic level, as a synonym of the former. Another name for the restricted genus based on Osche's *Rhabditis* must accordingly be sought.

2. *Tribactis* Dujardin [1844].

This name was used without description, definition, or indication, by Dujardin (1844) on page 3 of his *Histoire Naturelle des Helminthes* . . . and later in the book (p. 653) suppressed as an alternate name for *Rhabditis* (pp. 239–243). In its first use it was thus a *nomen nudum*, and in its second a junior objective synonym, by page priority, of *Rhabditis*, taking the same species, *R. terricola*, as type. Inasmuch as *Rhabditis* is a valid name, *Tribactis* falls as a synonym.

3. *Leptoderes* Dujardin [1844] and *Leptodera* Dujardin [1844].

Leptoderes in relation to *Leptodera* shares the same fate as *Tribactis* in relation to *Rhabditis*. The former was used as a *nomen nudum* on p. 2 and suppressed as a synonym of *Leptodera* (pp. 108–109) on p. 653. The latter genus was erected for a single species, hence type (by indication—monotypy), *L. flexilis* Dujardin [1844]—an internal parasite of the slug "*Limax cinereus*" (= *Limax maximus* Linné, 1758). However, both *Leptodera* and *Leptoderes* of Dujardin are respective junior homonyms of *Leptodera* and *Leptoderes* of Audinet-Serville (1838), who used these names alternatively for a genus of

orthopteroid insects. Therefore both names of Dujardin are unavailable. Chitwood (1935a) renamed the nominal genus *Leptodera* Dujardin [1844], *Agfa*. Further discussion of the nomenclature of *Agfa* and of its type, *Leptodera flexilis*, will be found under *Agfa* in chronological order. (See also the discussion of *Leptodora* Dewitz, 1892, under section 7.).

4. *Ascaroides*, Barthélemy, 1858.

Barthélemy (1858, p. 45) found nematode larvae in the eggs of a "grey slug"⁵ and followed their development from an early stage to what he considered the adult state (but what appears from his description and figure (pl. 5, fig. 9) to have been a subadult or late larval stage of female sex, in which the gonads had begun to develop). To these larvae he gave the new name *Ascaroides limacis*, thus establishing a new genus *Ascaroides* with *A. limacis* Barthélemy, 1858, as type (by indication—monotypy). Many authors, of whom Goodey (1951) and Osche (1952) are among the most recent, have held this genus to be a synonym of *Rhabditis*. This assumption, however, appears to be in error, for Chitwood and Chitwood (1937a) reported the finding of very similar larvae in the eggs of the slug "*Deroceras agreste*" (= *Deroceras reticulatum* (Müller, 1774) Pilsbry, 1948) and identified these as deriving from adults living in the gut of the slug and apparently belonging to species of the genus *Cosmocercoides* Wilkie, 1930 (suborder Ascaridina), most known representatives of which occur in amphibians. It is quite likely that Barthélemy's "grey slug" was also *D. reticulatum*, for this is a very common European slug of grey color. It has been introduced widely into the New World (see Pilsbry, 1948, p. 533), and it is thus possible that Chitwood and Chitwood rediscovered *A. limacis*. However, Dujardin, in describing *Leptodera flexilis*, referred to its host, *Limax maximus*, as a "*limace grise*"; so apparently the identity of Barthélemy's slug host cannot be definitely asserted.

Chitwood (1933a) and Chitwood and Chitwood (1937a) regarded the genus *Trionchonema* Kreis, 1932, as being synonymous with *Cosmocercoides*; the type of the former, *T. rusticum* Kreis, 1932 (= *Cosmocercoides rustica* (Kreis, 1932) Chitwood, 1938) is, to my knowledge, the only described and named cosmocercid inhabiting snails exclusively, unless *Ascaroides limacis* is to be placed in the same group. *T. rusticum* was described from a snail that Kreis (1932a)

⁵ "Limace grise."

recorded as "*Polygyra espicola*" [sic] (= *Polygyra postelliana* (Bland, 1859) Binney, 1878), but which probably was *Polygyra auriformis* (Bland, 1859) Binney, 1878. Chitwood and Chitwood (1937a) have also reported a cosmocercid—unidentified as to species in this case—from a snail host, "*Opeas goodalli*" (= *Opeas pumilum* (Pfeiffer, 1840) Pilsbry, 1910). Very recently Ogren (1953) has recorded from a number of snails and slugs the species *Cosmocercoides dukae* (Holl, 1928) Wilkie, 1930, originally described from a salamander. Apparently one or more species of *Cosmocercoides* are widespread in terrestrial pulmonates.

The immature specimen of *A. limacis* figured by Barthélemy agrees in general structure with the supposition of cosmocercid affinities, and in view of Chitwood and Chitwood's observation there appears no reasonable doubt that it belongs in the family Cosmocercidae Travassos, 1925. It would therefore appear not unlikely that, if *A. limacis* can be identified and properly described, *Cosmocercoides*, unless preserved by the International Commission, should fall as a synonym of *Ascaroides*.

In any event, the genus *Ascaroides* Barthélemy, 1858, having been removed from the Rhabditina to the Ascaridina, its name is not a candidate for any of the genera deriving from Osche's subgenera.

5. *Pelodytes* Schneider, 1859.

This genus was erected by Schneider (1859, p. 178) for a single species, hence type (by indication—monotypy), *Pelodytes hermaphroditus* Schneider, 1859, an hermaphroditic species, found in decaying snails, of which Schneider found no males. The name *Pelodytes* Schneider, 1859, falls as a junior homonym of *Pelodytes* Bonaparte, 1841 (Amphibia). Nevertheless, it is desirable to determine, if possible, to what present genus the name *Pelodytes* of Schneider (1859) correctly applies. Schneider subsequently (1866, p. 315) renamed *P. hermaphroditus*, *Leptodera foecunda* and figured the head and tail of the hermaphrodite. This species has been essentially ignored except for a passing remark by Maupas (1900) in his description of a purportedly new species, *Rhabditis caussaneli*. Maupas pointed out that both *L. foecunda* and *R. caussaneli* were found in snails and that one might be tempted to consider them the same, but for the fact that the configuration and proportions of the tail of *L. foecunda* were very different from those of *R. caussaneli*. Actually, however, on comparison

of Schneider's and Maupas' descriptions and figures and making allowance for the semi-diagrammatic nature of the former's figures, I find the agreement of the two nominal species to be very close. Particularly striking is the similarity of the stoma, with its prominent metastom, and of the esophagus. Maupas found only 1.4 ♂♂ per 1000 ♀♀; and Schneider could easily have overlooked rare males in his cultures. Osche provides additional evidence, for no other hermaphroditic species treated by him presents the combination of stomatal and tail characters of *R. caussaneli*.

I therefore believe that *Pelodytes hermaphroditus* (synonym *Leptodera foecunda*) and *R. caussaneli* are one and the same species and that the latter name must fall as a synonym of the former. At the generic level *Pelodytes* is therefore a synonym of *Rhabditis* (*sensu novo*), for *P. hermaphroditus* and *R. terricola* (*sensu novo*) are members of the same subgenus of Osche—*Choriorhabditis*—and are therefore congeneric in the genus *Rhabditis* as newly constituted here.

6. *Pelodera* Schneider, 1866.

This genus was erected by Schneider (1866, pp. 148–154) with four species *P. stronglyloides* (Schneider, 1860) Schneider, 1866 (= *Pelodytes stronglyloides* Schneider, 1860), *P. teres* Schneider, 1866, *P. papillosa* Schneider, 1866, and *P. pellio* Schneider, 1866. At the same time the generic name *Pelodytes* was discarded and the original type species of the genus so-named—*P. hermaphroditus*—was transferred to the genus *Leptodera* Dujardin [1844] and renamed *L. foecunda*, as already noted. It can therefore be argued that the taxonomic genus *Pelodera* is quite different from the taxonomic genus *Pelodytes*. Insofar as Schneider's treatment of *Pelodera* in 1866 is concerned, this is true, but the nomenclatorial consequences of his actions might be construed quite differently. By the International Rules a nominal genus specifically proposed as a substitute for a previous nominal genus must take the same species as type. If it were true that, in proposing the generic name *Pelodera*, Schneider had renamed *Pelodytes*, then *Pelodytes hermaphroditus* would automatically become type of *Pelodera*. This is the interpretation of Stiles and Hassall (1920).

However, I take issue with this assumption. What Schneider actually said at the end of his description of *Pelodera stronglyloides* (Schneider, 1860) Schneider, 1866 (p. 153), was: "I have discarded

the generic name *Pelodytes* as preoccupied."⁶ He did not say that, in proposing *Pelodera*, he was renaming *Pelodytes*; and, more significantly, he did not list *Pelodytes* in the synonymy of *Pelodera* (p. 148). I therefore hold that *Pelodera* Schneider, 1866, is not *Pelodytes* Schneider, 1859, renamed, and consequently that the determination of type for the later genus is quite independent of the determination of type for the earlier.

In 1905 Stiles and Hassall, believing incorrectly that *Pelodytes strongyloides* Schneider, 1860, was the only original species, hence type, of a genus *Pelodytes* Schneider, 1860, stated that this species was consequently type of *Pelodera* Schneider, 1866, which they held to be *Pelodytes* renamed. (Later, in 1920, they recognized the earlier *Pelodytes hermaphroditus* Schneider, 1859.) Now, despite the fact that their premises were erroneous both as regards *Pelodytes strongyloides* as type of *Pelodytes* and as regards *Pelodera* as *Pelodytes* renamed, the facts remain that *P. strongyloides* was an originally included species in *Pelodera* and that Stiles and Hassall in effect selected it as type of this genus. Theirs was the first such selection, and it accordingly stands.

Since *P. strongyloides* is a species in Osche's subgenus containing *Pelodera teres*, we therefore have a valid generic title for the genus resulting from the elevation of the subgenus *Rhabditis* (*sensu* Osche) to generic rank—a genus to which the name *Rhabditis* can no longer apply, as we have seen. This genus is consequently *Pelodera* Schneider, 1866, with type species *Pelodytes strongyloides* Schneider, 1860.

7. *Leptodora* Dewitz, 1892.

This name was used by Dewitz (1892, p. 139) as an obvious error for *Leptodera* of Schneider (1866), which is nomenclatorially equivalent to *Leptodera* Dujardin [1844]. It cannot, however, be used in place of *Leptodera*, for it is a junior homonym of *Leptodora* Lilljeborg, 1860 (Crustacea).

8. *Cruznema* Artigas, 1927.

This genus was established by Artigas (1927, p. 209) with a single species designated as type—*Cruznema cruznema* Artigas, 1927, a parasite in an unidentified millipede. Chitwood (1933b) considered this to be a synonym of *Rhabditis lambdiensis* Maupas, 1919.

⁶ "Den Gattungsnamen *Pelodytes* habe ich als bereits vergeben, fallen lassen."

Skriabin *et al.* (1954) place *Cruznema* in the suborder Ascaridina, but I believe that this is wrong and that Chitwood was correct. *R. lambdiensis* is consubgeneric with *Pelodytes strongyloides* in Osche's scheme, and therefore at the generic level *Cruznema* falls as a synonym of *Pelodera*.

9. *Cephaloboides* Rahm, 1928.

Cephaloboides was established as a subgenus of *Rhabditis* by Rahm (1928, p. 241) for a single new species *Rhabditis musicola* Rahm, 1928—hence type (by indication—monotypy). A figure and a more extended description of this species were provided by Rahm in a second paper (1929). Osche does not mention the subgenus, but lists *R. musicola* as an unverified species of *Rhabditis* (i.e., one for which the literature was not available to him).

Recently Osche has informed me (*in litt.*) that *Rhabditis pseudoxycerca* Goodey, 1929, must fall as a synonym of *R. musicola*. The latter thus belongs in the genus *Rhabditis* (*sensu stricto*), and therefore the subgeneric name *Cephaloboides* falls at the generic level as a synonym of *Rhabditis*.

10. *Diploscapteroides* Rahm, 1928.

This genus was established by Rahm (1928, p. 244) for a single new species, *Diploscapteroides brevicauda* Rahm, 1928—hence type (by indication—monotypy). As with *Rhabditis musicola* a figure and more extended description of the species were provided by Rahm in a second paper (1929). Osche lists this genus as a synonym of *Rhabditis*, but inconsistently makes no mention of *D. brevicauda*.

In my recent short paper I tentatively accepted *Diploscapteroides* in the Rhabditinae. However, on reviewing Rahm's descriptions, Osche (*in litt.*) now believes that it probably belongs in the Cephalobidae.

11. *Rhabditoides* Goodey, 1929 (March).

This genus was formed by Goodey (1929, p. 27) for its designated type *Rhabditoides coprophaga* Goodey, 1929. Sachs (1950) has shown that *R. coprophaga* is a synonym of *Rhabditis longispina* Reiter, 1928, which in turn was designated by Osche as type of his subgenus *Telorhabditis*. It therefore follows that *Telorhabditis* falls as a synonym of *Rhabditoides*, which is thus the correct name for the genus resulting from the elevation of Osche's subgenus *Telorhabditis* to generic status.

12. *Rhabditella* Cobb, 1929 (July).

Rhabditella was established as a subgenus of *Rhabditis* Cobb (1929, p. 263) for the single species, *Rhabditis leptura* Cobb, 1929, which he designated as type. It was raised to generic status by Chitwood (1933a). Osche has concluded that *R. leptura* is a synonym of *Rhabditis octopleuræ* Steiner, 1929⁷ (February). This in his system is con-subgeneric with *R. terricola* (syn. *R. aspera*), which is type of the genus *Rhabditis* (sensu novo). It therefore follows that at the generic level *Rhabditella* falls as a synonym of *Rhabditis*.

13. *Pseudorhabditis* Kreis, 1929, and *Asymmetricus* Kreis, 1930.

Asymmetricus was established by Kreis (1930) for two species, *Pseudorhabditis acuminatus* [sic] Kreis, 1929, and *P. labiatus* [sic] Kreis, 1929; it was *Pseudorhabditis* Kreis, 1929 (*non* Perroncito, 1880) renamed. No type was designated or indicated for either *Asymmetricus* or *Pseudorhabditis*, and none has subsequently been selected, although Gutiérrez (1949) has recently discussed *Asymmetricus*—concluding, erroneously, that it must be regarded as “*incertae sedis*.”

Goodey (1951) placed both species in the genus *Tricephalobus* Steiner, 1936, along with the type thereof—*T. longicaudatus* Steiner, 1936⁸. However, *P. acuminatus* appears most likely to belong with the group of species placed by Osche in his subgenus *Mesorhabditis*. *P. labiatus* on the other hand is indeed a cephalobid, but according to Thorne (*in litt.*) it belongs in the genus *Acrobeloides* Cobb, 1924⁹.

In order to protect the name *Mesorhabditis* I hereby select the cephalobid species, *P. labiatus* Kreis, 1929, as type of the genus *Asymmetricus* Kreis, 1930. The consequence of this is that, inasmuch as *Acrobeloides* Cobb, 1924, has priority over *Asymmetricus* Kreis, 1930, the latter falls as a junior subjective synonym of the former for so long as their respective types—*Cephalobus bütschlii* de Man, 1884, and *Pseudorhabditis labiatus* Kreis, 1929—are treated as being congeneric.

14. *Agfa* Chitwood, 1935.

As mentioned under section 3, Chitwood (1935a, p. 53) renamed the genus *Leptodera* Dujardin [1844] *Agfa* in order to provide a valid generic title for the taxonomic genus containing *Leptodera flexilis* Dujardin

⁷ 1929b.⁸ 1936a.⁹ 1924a.

[1844] as type; he designated this species as type of the new nominal genus. Osche does not mention *Agfa*, nor does he list *L. flexilis* as a species of *Rhabditis* (*sensu lato*), but inconsistently (from the nomenclatorial point of view) he lists *Leptodera* as a synonym of *Rhabditis*.

L. flexilis was well described and figured by Dujardin (1844) and independently found, described, and figured by Schneider (1866). No subsequent worker has redescribed it, although one is led to suspect on the basis of Schneider's discussion (pp. 156-157) that it must be a common parasite in *Limax maximus*. However, Mengert (1958) has failed to rediscover it in her extensive investigation of slug and snail nematodes. It presents unusual features that appear to make impossible the inclusion of the genus in any of the established families of the superfamily Rhabditoidea Travassos, 1920. Therefore *Agfa* cannot enter into consideration as a generic name for any of Osche's subgenera raised to genera, and Osche errs in listing *Leptodera* (= *Agfa*) as a synonym of *Rhabditis* (*sensu lato*).

The establishment of the systematic position of *Agfa* is worth attempting. In its long tubular stoma and rayed male bursa it appears rhabditoid (suborder Rhabditina) rather than ascaridoid (suborder Ascaridina, wherein it might be suspected to fall). The families of the Rhabditoidea, as recognized by Chitwood (1950), are eight in number: Rhabditidae Örley, 1880, Cylirocorporidae Goodey, 1939, Rhabdiasidae Railliet, 1915, Angiostomatidae (Blanchard, 1896), Steiner-nematidae Chitwood and Chitwood 1937,¹⁰ Diplogasteridae Steiner, 1929,¹¹ Strongyloididae Chitwood and McIntosh, 1934, and Cephalobidae Chitwood and Chitwood, 1934. The long, apparently simple, tubular stoma of *Agfa* excludes it from all of these families except Rhabditidae and Cylirocorporidae. But, though it agrees with the latter in having its esophagus terminating in a nonvalvulated bulb, it disagrees from both in having no anterior esophageal swelling representing the corpus and from the former in its lack of esophageal valves.

Although *Agfa* might be placed in a new subfamily of the Cylirocorporidae by modification of the diagnosis of this family, the best solution appears to be to erect a new family Agfidae for the single (type) genus *Agfa* Chitwood, 1935. The relatively large size (females up to 6 mm.) of the species *Agfa flexilis* (Dujardin [1844]) Chitwood, 1935, suggests a considerable period of evolution as a parasite. It is to be hoped that the establishment of this family will stimulate the

¹⁰ 1937b.

¹¹ 1929a.

rediscovery of *A. flexilis* and the elucidation of its anatomy. A diagnosis for the new family follows:

Agfidae fam. nov.

Rhabditoidea: ?2 lateral lips; stoma relatively long and tubular, without glottoid apparatus; esophagus without a defined corpus and terminating in a pyriform bulb without valves. Female with two ovaries and approximately equatorial vulva; male leptoderan, with 5 (?6) pairs of genital papillae and a bursa consisting of short lateral alae. (Parasitic in the reproductive tract of a slug.)

15. *Parasitorhabditis* Fuchs, 1937.

Fuchs (1937, p. 294) established a subgenus *Parasitorhabditis*, which he placed in the genus *Rhabditis*, for a single nominal species—hence type (by indication—monotypy) *Rhabditis obtusa* Fuchs, 1915. This species was divided by him taxonomically (1915, 1937) into many "formae." Chitwood (1950) and I have been the only ones to raise *Parasitorhabditis* to generic rank; Osche considers it merely as one of the eight subgenera of the genus *Rhabditis* (*sensu lato*).

Fuchs, despite his clear statement that *Parasitorhabditis* was a subgenus, incorrectly, but consistently referred to *R. obtusa* as *Parasitorhabditis obtusa* throughout his paper. The question arises as to whether one should attribute to him the combination *Parasitorhabditis obtusa*. I take the view that one should not, but the International Rules admittedly do not yet cover this point explicitly.

16. *Cuticularia* van der Linde, 1938.

This genus was erected by van der Linde (1938, p. 11) for *Cuticularia mathesoni* van der Linde, 1938—a species based on two males and six females found in sphagnum in New York State. Dr. Osche has examined the figures and informs me (*in litt.*) that this species is a synonym of *Rhabditis oxycerca* de Man, 1895. The latter falls in the genus *Rhabditis* (*sensu stricto*), and therefore at the generic level *Cuticularia* falls as a synonym of *Rhabditis*.

17. *Epimenides* Gutiérrez, 1949.

Epimenides extricatus Gutiérrez, 1949, type and only species of *Epimenides* Gutiérrez, 1949, is a synonym of *Rhabditis lambdiensis*

Maupas, 1919, which in the scheme followed here falls in the genus *Pelodera* Schneider, 1866. Therefore *Epimenides* falls as a synonym of *Pelodera*.

II. THE GENERA AND SUBGENERA OF THE RHABDITINAE.

Aside from the present author (Dougherty, 1953) the three most recent workers to treat the genera of the Rhabditinae (in the modern sense) are Chitwood (1950a), Goodey (1951), and Osche (1952). The first of these lists the rhabditin genera (without evaluation) as *Rhabditis*, *Cruznema*, *Rhabditella*, *Rhabditoides*, *Parasitorhabditis*, and *Brevibucca*. In the new system adopted here the second and third of these genera fall as synonyms of *Pelodera* and *Rhabditis*, respectively. Goodey considers the genera of the Rhabditinae to be *Rhabditis*, *Rhabditella*, *Brevibucca*, *Rhabditoides*, and *Cheilobus* (neither *Cruznema* nor *Parasitorhabditis* being listed in the synonymy of any of the other genera, however). Of Goodey's genera Osche accepts *Rhabditis*, *Brevibucca*, and *Cheilobus* and rejects *Rhabditella* and *Rhabditoides* as synonyms of *Rhabditis*. Recently a genus *Pararhabditis* has been established by Schuurmans Stekhoven (1951) with a single species, *P. flagellicaudatus* [sic] Schuurmans Stekhoven, 1951, which he designates as type. The generic name is, however, a homonym of *Pararhabditis* Baylis and Daubney, 1926, and has more recently been changed to *Neorhabditis* by Schuurmans Stekhoven (1954).

It therefore follows that, in addition to eight genera based on the eight subgenera of Osche, three other genera must be considered in connection with the subfamily Rhabditinae—namely, *Cheilobus* Cobb, 1924,¹² *Brevibucca* Goodey, 1935, and *Neorhabditis* Schuurmans Stekhoven, 1954.

Chitwood (1950a) has placed *Cheilobus* along with another nominal genus, *Rhabditophanes* Fuchs, 1930, in the family Cephalobidae (subfamily Alloionematinae Chitwood and McIntosh, 1934). Goodey has given adequate reasons for the synonymizing of *Cheilobus* and *Rhabditophanes*; he has not, however, recognized that Cobb's *Cheilobus* is an invalid homonym of *Cheilobus* Rafinesque, 1817 (Pisces), and that consequently *Rhabditophanes* must be used in its place.

Unlike Chitwood and Goodey I do not feel sure that *Brevibucca* should be regarded as a rhabditin genus, but I do agree with Chitwood

¹² 1924b.

that *Rhabditophanes* (syn. *Cheilobus*) does not belong in the Rhabditidae.

Osche (*in litt.*) informs me that it is impossible to allocate the genus *Neorhabditis* on the basis of the description or figures of the single female upon which the species and hence genus were established. It is not here accepted in the Rhabditinae.

Therefore, if we tentatively accept *Brevibucca* in the Rhabditinae, we have some nine genera in the subfamily. This is as I have recently constituted the subfamily (Dougherty, 1953) except for the relegation of *Brevibucca* to uncertain status and the elimination of *Diploscapteroides*.

We may now turn our attention to the constitution of Osche's two largest subgenera, *Rhabditis* and *Choriorhabditis*, in which he recognizes four and five "species-groups" respectively. If his subgenera merit generic rank, these groups may justifiably be considered subgenera as I have already done (Dougherty, 1953). Certain names that must be suppressed as synonyms at the generic level have consequently come into use at the subgeneric; in other cases new names have been necessary. It is more than likely that one or more of these subgenera themselves deserve generic status, but I leave to future work decision in such matters. In proposing needed new subgeneric names I arbitrarily took the first two or three syllables of the specific names used by Osche to designate the equivalent species-groups and combined them with the suffix *-dera* or *-ditis*, as appropriate; no pretense was intended that this is classically esthetic or meaningful. It is now necessary to suppress the name *Curviditis* Dougherty, 1953, as a junior subjective synonym of *Cephaloboides* Rahm, 1928, inasmuch as the type species of the respective subgenera—*Leptodera curvicaudata* Schneider, 1866, and *Rhabditis musicola* Rahm, 1928—are consubgeneric in the scheme adopted here. The nominal genus *Cuticularia* van der Linde, 1938, also falls at the subgeneric level as a synonym of *Cephaloboides*, inasmuch as the type of the former—*Cuticularia mathesoni* van der Linde, 1938 (= *Rhabditis oxycerca* de Man, 1895)—is also consubgeneric with *R. musicola*.

It should be noted that at the subgeneric level the genus *Epimenides* Gutiérrez, 1949, falls as a synonym of *Cruznema* Artigas, 1927, since the type species of both are here considered synonymous.

Following are the genera and subgenera of the Rhabditinae—largely corresponding to Osche's subgenera and species-groups, respectively. Type species of these genera and subgenera are given in the list at the end of the next section.

GENERA AND SUBGENERA OF THE RHABDITINAE.

Revised Generic and Subgeneric Names.

Osche's Equivalents: Subgeneric and Species-group Names.

- | | |
|--|---|
| 1. <i>Pelodera</i> Schneider, 1866— | 1. <i>Rhabditis</i> (subgen. <i>sensu</i> Osche, 1952)— |
| a. <i>Pelodera</i> (Schneider, 1866) Dougherty, 1953. | a. <i>Teres</i> -group, of Osche, 1952. |
| b. <i>Cruzneina</i> (Artigas, 1927) Dougherty, 1953 (syn. <i>Epimenides</i> Gutiérrez, 1949). | b. <i>Lambdiensis</i> -group, of Osche, 1952. |
| c. <i>Coarctadera</i> Dougherty, 1953. | c. <i>Coarctata</i> -group, of Osche, 1952. |
| d. <i>Cylindridera</i> Dougherty, 1953. | d. <i>Cylindrica</i> -group, of Osche, 1952. |
| 2. <i>Rhabditis</i> Dujardin [1844] | 2. <i>Choriorhabditis</i> Osche, 1952— |
| a. <i>Rhabditis</i> (Dujardin [1844]) Osche, 1952. | a. <i>Maupasi</i> -group, of Osche, 1952. |
| b. <i>Pellioiditis</i> Dougherty, 1953. | b. <i>Pellio</i> -group, of Osche, 1952. |
| c. <i>Choriorhabditis</i> Osche, 1952. | c. <i>Longicaudata</i> -group, of Osche, 1952. |
| d. <i>Cephaloboides</i> Rahm, 1928 (syn. <i>Cuticularia</i> van der Linde, 1938; <i>Curviditis</i> Dougherty, 1953). | d. <i>Curvicaudata</i> -group, of Osche, 1952. |
| e. <i>Rhabditella</i> Cobb, 1929. | e. <i>Elongata</i> -group, of Osche, 1952. |
| 3. <i>Rhabditoides</i> Goodey, 1929. | 3. <i>Telorhabditis</i> Osche, 1952. |
| 1. <i>Caenorhabditis</i> (Osche, 1952) Dougherty, 1953. | 1. <i>Caenorhabditis</i> Osche, 1952. |
| 5. <i>Mesorhabditis</i> (Osche, 1952) Dougherty, 1953. | 5. <i>Mesorhabditis</i> Osche, 1952. |
| 6. <i>Teratorhabditis</i> (Osche, 1952) Dougherty, 1953. | 6. <i>Teratorhabditis</i> Osche, 1952. |

- | | |
|---|--|
| 7. <i>Protorhabditis</i> (Osche, 1952) Dougherty, 1953. | 7. <i>Protorhabditis</i> Osche, 1952. |
| 8. <i>Parasitorhabditis</i> (Fuchs, 1937) Chitwood, 1950. | 8. <i>Parasitorhabditis</i> Fuchs, 1937. |
| 9. <i>Incertae sedis</i> : <i>Brevibucca</i> Goodey, 1935. | 9. [Recognized as a genus by Osche]. |

III. THE SPECIES OF THE RHABDITINAE.

Osche has distributed some 126 rhabditin species¹³ in seven of the eight subgenera recognized by him. For the eighth—*Parasitorhabditis*—he provides no list of species, but refers to an unpublished manuscript by Rühm in which a number of species are apparently recognized; he does, however, mention by name two previously described species of this subgenus, thus bringing the total number for *Rhabditis* (*sensu lato*) to 128. Of these, certain are accepted conditionally—being regarded as probable or possible synonyms. Some 24 of the 128 species are not previously described; for three of these he gives complete descriptions and assumes authorship, but for the remaining 21 he gives only brief diagnostic features and attributes authorship to four of his colleagues at Erlangen—13 to Körner, five to Hirschmann, two to Rühm, and one to Mengert. Complete descriptions are to be found in the unpublished theses of these workers, which he cites in his bibliography and which presumably will eventually appear in print. (In fact the descriptions of Hirschmann (1952), Mengert (1953), and Körner (1954) have subsequently appeared; and I have seen the manuscript of the thesis of Rühm on a visit to Erlangen.) Publication of these names in such a way by Osche is much to be regretted, for, insofar as they represent recognizable species, they must be accorded priority as of Osche's usage of them, with all the attendant difficulty of citing them. Moreover, without additional information some at least of these species are possibly unrecognizable. One example is particularly unfortunate: Osche takes as type of *Protorhabditis* the species *Rhabditis xylocola* Körner in

¹³ He first lists (pp. 254–255) some 164 nominal species, plus two varieties, in alphabetical order, but of these 16 are suppressed as synonyms, 19 are of uncertain status (descriptions for 15 not seen by Osche), and three are transferred out of the Rhabditidae. (In a second subsidiary list he gives seven names as representing "uncertain *Rhabditis* species," of which four have already appeared in the primary list. Thus Osche actually treats 167 nominal species—22 of uncertain status.) He then relists the remaining 126 under their respective subgenera, with brief characterizations for most (pp. 256–267). Finally he provides a key (pp. 268–272) for some 79 species or groups of species, totalling 98 species in all.

Osche, 1952, for which almost the only information provided is: "Similar to the foregoing species. Lips simple, spicule not bent distally, more slender than in *R. postneri*."¹⁴ *R. postneri* Körner in Osche, 1952—the "foregoing species" in this case—is defined only as having: "V-shaped lip-supports similar to those of *Teratorhabditis*."¹⁵ A few other features of these two species can be deduced from the key that Osche provides for species of *Rhabditis*. Nevertheless, *Proto-rhabditis*, whether regarded as subgenus or genus, will not be established securely until a more extended description of *R. xylocola* is published. (This description is now available with the publication of Körner's monograph (1954).)

To the 128 species taxonomically located by Osche I am adding 15 here (marked with an asterisk (*) in the following lists)—four of these having been listed as unverified or unaccepted by Osche (marked with a double dagger (‡)), the other 11 having not been listed by him; and from the 128 I am dropping three, bringing the total number of species accepted in the Rhabditinae to 140. I am in addition changing the names used by Osche in five cases (marked with a dagger (†))—two of the replacement names having been listed as unverified (‡) by Osche and one as a synonym of another on the list (i.e. "*R. teres* . . . (= *R. terricola* . . .)") and two not having been listed by him at all. Most of these changes have been made possible by the kind cooperation of Dr. Osche, who has reviewed previously available articles in the original or in microfilm or photostat form and communicated his decisions and opinions to me. It has thus been possible to classify 14 of the 15 nominal species listed by him, but recorded as not having been seen; of these, eight have been found to fall outside the Rhabditinae. However, I have been able to allocate but one of the seven nominal species of which the descriptions were seen by him, but which were treated as unallocatable. In addition, 24 other nominal species of which the descriptions were previously unknown to Osche or which were previously not listed by him as rhabditid forms are here treated. 19 of these are allocated—11 as valid rhabditid species (as already mentioned), six as falling as synonyms of rhabditid species, and two as outside the Rhabditinae. Finally, five species not treated by Osche appear impossible of allocation at this time because of the inadequate descriptions so far published.

¹⁴ "Ähnlich der vorigen Art. Lippen einfach, Spiculum nicht distal gekerbt, schlanker als bei *Rh. postneri*."

¹⁵ "*Teratorhabditis*-ähnliche V-förmige Lippenstützen."

The foregoing changes are summarized in the following five lists :

ADDITIONS TO OSCHE'S LIST (1952) OF VALID SPECIES.

As originally published.

As used here.

- | | |
|--|---|
| 1. <i>*Brevibucca frugicola</i> Goodey [1948]. | 1. Same. |
| 2. <i>*Brevibucca saprophaga</i> Goodey, 1935. | 2. Same. |
| 3. <i>*Pseudorhabditis acuminatus</i> [sic] Kreis, 1929. | 3. <i>*?Mesorhabditis acuminata</i> (Kreis, 1929) comb. nov. |
| 4. <i>*Rhabditis belari</i> Nigon, 1949. | 4. <i>*Mesorhabditis belari</i> (Nigon, 1949) Dougherty, 1953. |
| 5. <i>*Rhabditis boettgeri</i> Meyl, 1953 ¹⁶ . | 5. <i>*Teratorhabditis boettgeri</i> (Meyl, 1953) comb. nov. |
| 6. <i>‡*Rhabditis briggsae</i> Dougherty and Nigon, 1949 ¹⁷ . | 6. <i>‡*Caenorhabditis briggsae</i> (Dougherty and Nigon, 1949) Dougherty, 1953. |
| 7. <i>*Rhabditis carpathicus</i> [sic] Soós, 1941. | 7. <i>*Caenorhabditis carpathica</i> (Soós, 1941) comb. nov. |
| 8. <i>‡*Rhabditis coffeae</i> , Rahm, 1928. | 8. Same (subgenus <i>Pellioiditis</i>). |
| 9. <i>*Rhabditis inarimensis</i> Meyl, 1953 ¹⁸ . | 9. <i>*Mesorhabditis inarimensis</i> (Meyl, 1953) comb. nov. |
| 10. <i>*Rhabditis insolita</i> Paesler, 1941. | 10. Same (subgenus <i>Pellioiditis</i>). (? syn. <i>R. hartmanni</i> Sachs, 1950). |
| 11. <i>‡*Rhabditis kowalewskyi</i> Golovin, 1901. | 11. <i>‡*Caenorhabditis kowalewskyi</i> (Golovin, 1901) comb. nov. |

¹⁶ 1953b.

¹⁷ Osche has synonymized this species with *Rhabditis clavopapillata* Kreis and Faust, 1933, but I cannot accept this as proved although it is possibly true. As originally described, *R. clavopapillata* has certain consistently different bursal characters from those of *R. briggsae* (see Nigon and Dougherty, 1949); even though these are minor, they may well be definitive, for the species of *Caenorhabditis* in general tend to be very similar to one another. Moreover, *R. clavopapillata* was recorded as growing well at 26°C., a temperature at which meiotic anomalies are induced in *R. briggsae*. Therefore, in my nutritional studies I shall continue to adhere to the specific name *briggsae* unless convincing evidence against this comes to hand. (See ADDENDA, under "Miscellaneous," for discussion of recent note by Osche (1954b) on this point.)

¹⁸ 1953a.

- | | |
|--|---|
| 12. <i>*Rhabditis longespiculosa</i> Schuurmans Stekhoven, 1951 | 12. <i>*Mesorhabditis longespiculosa</i> (Schuurmans Stekhoven, 1951) comb. nov. |
| 13. <i>*Rhabditis minutus</i> [sic] Cobb, 1893 ¹⁹ . | 13. <i>*Protorhabditis minuta</i> (Cobb, 1893) comb. nov. |
| 14. ‡ <i>*Rhabditis typica</i> Stefański, 1922 ²⁰ . | 14. ‡ <i>*Pelodera typica</i> (Stefański, 1922) comb. nov. (subgenus <i>Pelodera</i>). |
| 15. <i>*Rhabditis verneti</i> Maupas, 1900 ²¹ . | 15. Same (subgenus <i>Rhabditis</i>). |

DELETIONS FROM OSCHE'S LIST.

As originally published.

Disposition.

- | | |
|--|---|
| 1. <i>Rhabditis johnsoni</i> Micoletzky, 1922 ²² . | 1. Syn. of <i>R. maupasi</i> Seurat in Maupas, 1919. |
| 2. <i>Rhabditis leptodera</i> Hertwig, 1922 ²² . | 2. Syn. of <i>R. maupasi</i> Seurat in Maupas, 1919. |
| 3. <i>Rhabditis simplex</i> Cobb, 1893 ¹⁹ . | 3. Not allocatable. |

¹⁹ 1893b.

²⁰ This species appears very close to *Pelodera strongyloides* (Schneider, 1860) Schneider, 1866, except that it was figured as having unfused spicules, which, if accurately depicted, would place it in the genus *Rhabditis* (*sensu stricto*).

²¹ P. 468 (footnote); based on hermaphrodites described by Vernet (1872) under the name of *R. terricola*.

²² Although listed as separate species by Osche, the nominal species *R. johnsoni* and *R. leptodera* must fall as synonyms of the nominal species *R. maupasi* Seurat in Maupas, 1919, inasmuch as all of these are explicitly *R. pellio* of Bütschli (1873) renamed, even though the specimens actually studied by Johnson (1913), Maupas (1919), and Hertwig (1922) in one, two, or all three of the cases may not have been Bütschli's form. Further study is needed to establish how many species exist in this series of closely related forms. It appears likely that there are at least two dioecious forms (to one of which all hitherto proposed names—*R. maupasi*, *R. johnsoni* and *R. leptodera*—must be restricted) and one hermaphroditic form (for which the earliest available name is probably *R. verneti* Maupas, 1900). However, the possibility exists that both dioecious and hermaphroditic strains exist for certain species (e.g., *R. verneti*, or *R. maupasi*).

CHANGES OF NAMES USED BY OSCHE.

As used by Osche.

1. *Rhabditis limicola* Hirschmann
in Osche, 1952.
2. *Rhabditis aspera* Bütschli,
1876.
3. *Rhabditis caussaneli* Maupas,
1900.
4. *Rhabditis pseudoxycerca*
Goodey, 1929.
5. *Rhabditis elongata* (Schneider,
1866) Örley, 1880 [syn.
Leptodera elongata Schneider,
1866 (non Baird, 1858)].

As used here.

1. ‡†*Pelodera chitwoodi* (Bassen,
1940) comb. nov.
2. †*Rhabditis terricola* Dujardin
[1844].
3. †*Rhabditis hermaephrodita*
(Schneider, 1859) comb. nov.
4. ‡†*Rhabditis musicola* Rahm,
1928.
5. †*Rhabditis axei* (Cobbold,
1884) comb. nov.

ALLOCATION OF SPECIES LISTED, BUT NOT ALLOCATED, BY OSCHE.

As originally published.

1. *Cuticularia mathesoni* van der
Linde, 1938.
2. *Leptodera macrolaima*
Schneider, 1866.
3. *Leptodera niellyi* Blanchard
[1886].
4. *Rhabditis agilis* von Linstow,
1876.
5. *Rhabditis aphodiorum* Wülker,
1921.
6. *Rhabditis cephaloides* Stefański,
1922.
7. ‡†*Rhabditis chitwoodi* Bassen,
1940.
8. ‡**Rhabditis coffeae* Rahm,
1928.
9. *Rhabditis donbass* Skriabin,
Shul'ts, and Serbinov, 1926.

Present allocation.

1. To *Rhabditis* (syn. of *R.*
oxycerca de Man, 1895).
2. To *Cylindrocorpus* (family
Cylindrocorporidae).
3. Not allocatable (larval form).
4. Not allocatable.
5. Not allocatable (larval form).
6. To *Diploscapterinae* (family
Rhabditidae).
7. To *Pelodera* (syn. *R. limicola*
Hirschmann in Osche, 1952).
8. To *Rhabditis* (? syn. of *R.*
pellioides Bütschli, 1873).
9. To *Pelodera* (syn. of *P. teres*
Schneider, 1866).

- | | |
|---|--|
| 10. <i>Rhabditis foecalis</i> Watanabe, 1920. | 10. To <i>Rhabditis</i> (syn. of <i>R. viguieri</i> Maupas, 1900). |
| 11. <i>Rhabditis gracilis</i> Shingareva, Demidova and Kudriantsev, 1928. | 11. To <i>Rhabditis</i> (syn. of <i>Rhabditis axei</i> (Cobbold, 1884) comb. nov.). |
| 12. <i>Rhabditis hambletoni</i> Pereira, 1937. | 12. To ?Oxyuroidea. |
| 13. <i>Rhabditis impar</i> Cobb, 1924 ¹² . | 13. Not allocatable. |
| 14. ‡* <i>Rhabditis kowalewskyi</i> Golovin, 1901. | 14. To <i>Caenorhabditis</i> . |
| 15. <i>Rhabditis macroura</i> von Linstow, 1879. | 15. Not allocatable. |
| 16. ‡* <i>Rhabditis minutus</i> [sic] Cobb, 1893. | 16. To <i>Protorhabditis</i> . |
| 17. ‡† <i>Rhabditis musicola</i> Rahm, 1928. | 17. To <i>Rhabditis</i> (syn. <i>R. pseudoxycerca</i> Goodey, 1929). |
| 18. <i>Rhabditis nudicapitata</i> Stefański, 1922. | 18. To <i>Rhabditis</i> (syn. of <i>R. oxycerca</i> de Man, 1895). |
| 19. <i>Rhabditis parateres</i> Cobb, 1924 ¹² . | 19. Not allocatable. |
| 20. <i>Rhabditis schachtliella</i> Skriabin and Shul'ts, 1926. | 20. To <i>Rhabditoides</i> (syn. of <i>Rhabditoides inermis</i> (Schneider, 1866) comb. nov.). |
| 21. ‡* <i>Rhabditis typica</i> Stefański, 1922. | 21. To <i>Pelodera</i> (?syn. of <i>P. strongyloides</i> (Schneider, 1860) Schneider, 1866). |
| 22. <i>Rhabditis varsaviensis</i> Stefański, 1922. | 22. Not allocatable. |

ALLOCATION OF SPECIES NOT LISTED BY OSCHÉ
AND NOT ACCEPTED HERE.

As originally published.

1. *Rhabditis allgénii* Johnston, 1938 (*R. australis* Allgén, 1932, renamed).

Present allocation.

1. Not allocatable (larval form).

- | | |
|---|--|
| 2. <i>Rhabditis australis</i> Allgén, 1932 (non Cobb, 1893) ²³ . | 2. Not allocatable (larval form). |
| 3. <i>Rhabditis campbelli</i> Allgén, 1947 (<i>R. australis</i> Allgén, 1932, renamed). | 3. Not allocatable (larval form). |
| 4. <i>Rhabditis gingivalis</i> Stefański, 1953. | 4. To <i>Tricephalobus</i> (family Cephalobidae). |
| 5. <i>Rhabditis glauxi</i> Allgén, 1951 ²⁴ . | 5. Not allocatable. |
| 6. <i>Rhabditis ikedai</i> Tadano, 1950. | 6. Syn. of <i>Rhabditis papillosa</i> (Schneider, 1866) Örley, 1880. |
| 7. <i>Rhabditis leuckarti</i> Vernet, 1872. | 7. To <i>Rhabditophanes</i> (family Cephalobidae). |
| 8. <i>Rhabditis longistoma</i> Stefański, 1922. | 8. To <i>Cylindrocorpus</i> (family Cylindrocorporidae). |
| 9. <i>Rhabditis parapapillosa</i> Schuermans Stekhoven, 1951. | 9. Syn. of <i>Rhabditis oxycerca</i> de Man, 1895. |
| 10. <i>Rhabditis scanica</i> Allgén, 1949. | 10. Syn. of <i>Mesorhabditis ocypodis</i> (Chitwood, 1935) comb. nov. |
| 11. <i>Rhabditis suecica</i> Allgén, 1951 ²⁵ . | 11. Not allocatable. |
| 12. <i>Rhabditis stålbergi</i> Allgén, 1950. | 12. Syn. of <i>Rhabditis oxycerca</i> de Man, 1895. |
| 13. <i>Rhabditis tenuicaudata</i> Menzel and Stefański in Stefański, 1917 ²⁶ . | 13. Syn. of <i>Rhabditis axei</i> (Cobbold, 1884) comb. nov. |
| 14. <i>Rhabditis usui</i> Watanabe, 1927. | 14. Syn. of <i>Rhabditis axei</i> (Cobbold, 1884), comb. nov. |

²³ 1893a.²⁴ 1951b.²⁵ 1951a.²⁶ Not in Osche's main list (1952, pp. 254-255), although referred to the synonymy of *R. elongata* (= *axei*) on p. 261; this synonymy was originally suggested by Chitwood (1930).

Following is a list of the 140 species here accepted (in a few cases tentatively) in the nine genera and nine subgenera of the Rhabditinae—with certain corrections in the spellings, authors, and dates given by Osche (1952).

SPECIES ACCEPTED IN THE RHABDITINAE

1. *Pelodera* Schneider, 1866 (19 species).

a. *Pelodera* (Schneider, 1866) Dougherty, 1953 (9 species).

- i *Pelodera* (*P.*) *plicata* (Völk, 1950) comb. nov.
- ii *Pelodera* (*P.*) *stammeri* (Völk, 1950) comb. nov.
- iii ‡*Pelodera* (*P.*) *chitwoodi* (Bassen, 1940) comb. nov.
- iv *Pelodera* (*P.*) *strongyloides* (Schneider, 1860) Schneider, 1866 (type sp. of genus and subgenus (by selection—Stiles & Hassall, 1905)).
- v ‡**Pelodera* (*P.*) *typica* (Stefański, 1922) comb. nov.
- vi *Pelodera* (*P.*) *teres* Schneider, 1866.
- vii *Pelodera* (*P.*) *punctata* (Cobb, 1914) comb. nov.
- viii *Pelodera* (*P.*) *conica* (Reiter, 1928) comb. nov.
- ix *Pelodera* (*P.*) *litoralis* (Skwarra, 1921) comb. nov.

b. *Cruznema* (Artigas, 1927) Dougherty, 1953 (2 species) (syn. *Epimenides* Gutiérrez, 1944).

- i *Pelodera* (*Cr.*) *lambdaiensis* (Maupas, 1919) Dougherty, 1953 (syn. *Cruznema cruznema* Artigas, 1927—type sp. of subgenus (by designation)).
- ii *Pelodera* (*Cr.*) *monhysteroideis* (Skwarra, 1921) comb. nov.

c. *Coarctadara* Dougherty, 1953 (5 species).

- i *Pelodera* (*Co.*) *coarctata* (Leuckart, 1891) Dougherty, 1953 (type sp. of subgenus (by designation)).
- ii *Pelodera* (*Co.*) *cystilarva* (Völk, 1950) comb. nov.
- iii *Pelodera* (*Co.*) *serrata* (Körner in Osche, 1952) comb. nov.
- iv *Pelodera* (*Co.*) *tretzeli* (Sachs, 1950) comb. nov.
- v *Pelodera* (*Co.*) *voelki* (Sachs, 1950) comb. nov.

d. *Cylindridera* Dougherty, 1953 (3 species)

- i *Pelodera* (*Cy.*) *cylindrica* (Cobb, 1898) Dougherty, 1953 (type sp. of subgenus (by designation)).
- ii *Pelodera* (*Cy.*) *kolbi* (Sachs, 1950) comb. nov.
- iii *Pelodera* (*Cy.*) *icosiensis* (Maupas, 1916) comb. nov.

2. *Rhabditis* Dujardin [1844] (67 species)a. *Rhabditis* (Dujardin [1844]) Osche, 1952 (17 species).

- i *R. (R.) brevispina* (Claus, 1862) Bütschli, 1873.
- ii †*R. (R.) terricola* Dujardin [1844] (type sp. of genus and subgenus (by selection—Stiles and Hassall, 1905); syn. *R. aspera* Bütschli, 1873).
- iii *R. (R.) maupasi* Seurat in Maupas, 1919.
- iv ■*R. (R.) verneti* Maupas, 1900.
- v *R. (R.) aberrans* Krüger, 1913.
- vi *R. (R.) anomala* Hertwig, 1922.
- vii *R. (R.) caulleryi* Maupas, 1919.
- viii *R. (R.) guignardi* Maupas, 1900.
- ix *R. (R.) lucianii* Maupas, 1919.
- x *R. (R.) terrestris* Stephenson, 1942.
- xi *R. (R.) marionis* Maupas, 1900.
- xii *R. (R.) wohlgemuthi* Völk, 1950.
- xiii *R. (R.) silvatica* Volz, 1951 (syn. *Rhabditis silvestris* Volz, 1951 (lapsus for *silvatica*)).
- xiv *R. (R.) gongyloides* Reiter, 1928.
- xv *R. (R.) insectivora* Körner in Osche, 1952.
- xvi *R. (R.) maxima* Völk, 1950.
- xvii *R. (R.) succaris* Clapham, 1930.

b. *Pellioiditis* Dougherty, 1953 (19 species).

- i *R. (P.) seurati* Maupas, 1916.
- ii *R. (P.) papillosa* (Schneider, 1866) Örley, 1880.
- iii *R. (P.) neopapillosa* Mengert in Osche, 1952.
- iv †*Rhabditis (P.) hermaphrodita* (Schneider, 1859) comb. nov. (syn. *R. caussaneli* Maupas, 1900).
- v *R. (P.) mairei* Maupas, 1919.
- vi *R. (P.) pellio* (Schneider, 1866) Bütschli, 1873 (type sp. of subgenus (by designation)).
- vii *R. (P.) pellioides* Bütschli, 1873.
- viii †**R. (P.) coffeae* Rahm, 1928.
- ix *R. (P.) bütschlii* de Man, 1876.
- x *R. (P.) friderici* Hirschmann in Osche, 1952.
- xi *R. (P.) fluviatilis* Bütschli, 1876.
- xii *R. (P.) craspedocerca* Völk, 1950.
- xiii *R. (P.) ehrenbaumi* Bresslau and Schuurmans Stekhoven in Schuurmans Stekhoven, 1935²⁷.
- xiv *R. (P.) velata* Bresslau and Schuurmans Stekhoven in Schuurmans Stekhoven, 1935²⁷.

²⁷ See also Bresslau and Schuurmans Stekhoven, 1940.

- xv *R. (P.) voighti* Rahm, 1925.
 - xvi *R. (P.) viguieri* Maupas, 1900.
 - xvii **R. (P.) insolita* Paesler, 1941.
 - xviii *R. (P.) hartmanni* Sachs, 1950.
 - xix *R. (P.) marina* Bastian, 1865²⁸.
- c. *Choriorhabditis* Osche, 1952 (23 species).
- i *R. (Ch.) longicaudata* Bastian, 1865 (type sp. of subgenus (by designation)).
 - ii *R. (Ch.) producta* (Schneider, 1866) Örley, 1880.
 - iii *R. (Ch.) paraelongata* Micoletzky, 1915.
 - iv *R. (Ch.) duthiersi* Maupas, 1900.
 - v *R. (Ch.) brassicae* Southern, 1909.
 - vi *R. (Ch.) körneri* Osche, 1952.
 - vii *R. (Ch.) macrospiculata* Stefański, 1916.
 - viii *R. (Ch.) uliginosa* Soós, 1938.
 - ix *R. (Ch.) cristata* Hirschmann in Osche, 1952.
 - x *R. (Ch.) acarta* Rühm in Osche, 1952.
 - xi *R. (Ch.) heteruroides* Altherr, 1938.
 - xii *R. (Ch.) dubia* Bovien, 1937.
 - xiii *R. (Ch.) heterurus* Örley, 1880.
 - xiv *R. (Ch.) gracilicauda* de Man, 1876.
 - xv *R. (Ch.) intermedia* de Man, 1880.
 - xvi *R. (Ch.) filiformis* Bütschli, 1873.
 - xvii *R. (Ch.) lepida* Kreis, 1929, emend. nov. (syn. *R. lepidus* Kreis, 1929).
 - xviii *R. (Ch.) pseudoelongata* Micoletzky, 1914.
 - xix *R. (Ch.) australis* Cobb, 1893²².
 - xx *R. (Ch.) guernei* Potts, 1910.
 - xxi *R. (Ch.) sechellensis* Potts, 1910.
 - xxii *R. (Ch.) lacustris* Micoletzky, 1914.
 - xxiii *R. (Ch.) sergenti* Maupas, 1916.
- d. *Cephaloboides* Rahm, 1928 (6 species) (syn. *Cuticularia* van der Linde, 1938; *Curviditis* Dougherty, 1953).
- i *R. (Ce.) curvicaudata* (Schneider, 1866) Örley, 1885.
 - ii *R. (Ce.) oxycerca* de Man, 1895 (syn. *Cuticularia mathesoni* van der Linde, 1938)—type sp. of genus *Cuticularia* van der Linde, 1938 (by designation)).
 - iii *R. (Ce.) armata* Fuchs, 1931.
 - iv *R. (Ce.) ciliata* Fuchs, 1931.

²⁸ See Osche (1954a).

- v *R. (Ce.) paraciliata* Goodey [1944].
- vi ††*R. (Ce.) musicola* Rahm, 1928 (type of subgenus (by indication—monotypy); syn. *R. pseudoxycerca* Goodey, 1929).
- e. *Rhabditella* Cobb, 1929 (2 species).
- i *R. (Rhabditella) octopleura* Steiner, 1929,⁷ Feb. (syn. *R. leptura* Cobb, 1929, July—type sp. of subgenus (by designation)).
- ii †*Rhabditis (Rhabditella) axei* (Cobbold, 1884) comb. nov. (syn. *Leptodera elongata* Schneider, 1866, non Baird, 1858; *Pelodera axei* Cobbold, 1884).
3. *Rhabditoides* Goodey, 1929 (6 species).
- a. *Rhabditoides longispina* (Reiter, 1928) Dougherty, 1953 (type sp. of genus (by designation)).
- b. *Rhabditoides incisocaudata* (de Coninck, 1935) comb. nov.
- c. *Rhabditoides inermiformis* (Osche, 1952) comb. nov.
- d. *Rhabditoides inermis* (Schneider, 1866) comb. nov.
- e. *Rhabditoides giardi* (Maupas, 1915) comb. nov.
- f. *Rhabditoides hermaphrodita* (Osche, 1952) comb. nov.
4. *Caenorhabditis* (Osche, 1952) Dougherty, 1953 (10 species).
- a. *Caenorhabditis elegans* (Maupas, 1900) Dougherty, 1953 (type sp. of genus (by designation)).
- b. **Caenorhabditis kowalewskyi* Golovin, 1901.
(? syn. of *C. elegans*^{28a}).
- c. **Caenorhabditis briggsae* (Dougherty and Nigon, 1949) Dougherty, 1953.
- d. *Caenorhabditis clavopapillata* (Kreis and Faust, 1933) comb. nov.
- e. *Caenorhabditis perrieri* (Maupas, 1900) comb. nov.
- f. *Caenorhabditis dolichura* (Schneider, 1866) comb. nov.
- g. *Caenorhabditis pseudodolichura* (Körner in Osche, 1952) comb. nov.
- h. *Caenorhabditis carpathica* (Soós, 1941) comb. nov.
- i. *Caenorhabditis debilicauda* (Fuchs, 1937) comb. nov.
- j. *Caenorhabditis rara* (Körner in Osche, 1952) comb. nov.

^{28a} Pp. 7-12 and pl. 3, figs. 5-8; see also Golovin (1902, pp. 142-144 and pl. 4, figs. 75, 76, and 81).

5. *Mesorhabditis* (Osche, 1952) Dougherty, 1953 (18 species).
 - a. *Mesorhabditis spiculigera* (Steiner, 1936)²⁹ Dougherty, 1953 (type sp. of genus (by designation)).
 - b. *Mesorhabditis oschei* (Körner in Osche, 1952) comb. nov.
 - c. *Mesorhabditis ultima* (Körner in Osche, 1952) comb. nov.
 - d. *Mesorhabditis tenuispicula* (Körner in Osche, 1952) comb. nov.
 - e. **Mesorhabditis longespiculosa* (Schuurmans Stekhoven, 1951) comb. nov.
 - f. *Mesorhabditis juglandicola* (Fuchs, 1937) comb. nov.
 - g. *Mesorhabditis monkhystera* (Bütschli, 1878) comb. nov.
 - h. *Mesorhabditis macrocheila* (Kreis, 1932)³⁰ comb. nov.
 - i. *Mesorhabditis cryptocercoides* (Wollenweber, 1921) comb. nov.
 - j. *Mesorhabditis ocypodis* (Chitwood, 1935)³¹ comb. nov.
 - k. *Mesorhabditis quercophila* (Rühm in Osche, 1952) comb. nov.
 - l. *Mesorhabditis graciliformis* (Goffart, 1935)³² comb. nov. (syn. *Rhabditis gracilis* Goffart, 1935;³³ non Shingareva, Demidova, and Kudriantsev, 1928).
 - m. *Mesorhabditis labiata* (Völk, 1950) comb. nov.
 - n. **Mesorhabditis belari* (Nigon, 1949) Dougherty, 1953.
 - o. *Mesorhabditis irregularis* (Körner in Osche, 1952) comb. nov.
 - p. *Mesorhabditis acris* (Bastian, 1865) comb. nov.
 - q. **Mesorhabditis inarimensis* (Meyl, 1953)¹⁸ comb. nov.
 - r. *Incertae sedis*: **Mesorhabditis acuminata* (Kreis, 1929) comb. nov.
6. *Teratorhabditis* (Osche, 1952) Dougherty, 1953 (4 species).
 - a. *Teratorhabditis dentifera* (Völk, 1950) Dougherty, 1953 (type sp. of genus (by designation)).
 - b. *Teratorhabditis coroniger* (Altherr, 1938) comb. nov.
 - c. *Teratorhabditis chitinolabiata* (Schneider, 1938) comb. nov.
 - d. **Teratorhabditis boettgeri* (Meyl, 1953)¹⁶ comb. nov.
7. *Protorhabditis* (Osche, 1952) Dougherty, 1953 (12 species).
 - a. *Protorhabditis xylocola* (Körner in Osche, 1952) Dougherty, 1953 (type sp. of genus (by designation)).
 - b. *Protorhabditis janeti* (de Lacaze-Duthiers in Janet, 1893) comb. nov.
 - c. *Protorhabditis oxyuris* (Claus, 1862) comb. nov.
 - d. *Protorhabditis ornata* (Bastian, 1865) comb. nov.

²⁹ 1936a.³⁰ 1932b.³¹ 1935b.³² 1935b.³³ 1935a.

- e. *Protorhabditis anthobia* (Schneider, 1988) comb. nov.
 - f. *Protorhabditis elaphri* (Hirschmann in Osche, 1952) comb. nov.
 - g. *Protorhabditis tristis* (Hirschmann in Osche, 1952) comb. nov.
 - h. *Protorhabditis virgo* (Körner in Osche, 1952) comb. nov.
 - i. *Protorhabditis postneri* (Körner in Osche, 1952) comb. nov.
 - j. *Protorhabditis parvoelata* (Körner in Osche, 1952) comb. nov.
 - k. *Protorhabditis rühmi* (Körner in Osche, 1952) comb. nov.
 - l. **Protorhabditis minuta* (Cobb, 1898)¹⁹ comb. nov.
8. *Parasitorhabditis* (Fuchs, 1937) Chitwood, 1950 (2 species).
 - a. *Parasitorhabditis obtusa* (Fuchs, 1915) Dougherty, 1958 (type sp. of genus (by indication—monotypy)).
 - b. *Parasitorhabditis ateri* (Fuchs, 1937) comb. nov.
 9. *Incertae sedis: Brevibucca* Goodey, 1935 (2 species).
 - a. **Brevibucca saprophaga* Goodey, 1935 (type sp. of genus (by designation)).
 - b. **Brevibucca frugicola* Goodey [1948].

IV. SUMMARY.

Nine genera, listed on pages 122–123 are recognized in the subfamily Rhabditinae Micoletzky, 1922, in place of three genera recognized by Osche (1952) in his recent revision of the genus *Rhabditis* Dujardin [1844] (*sensu lato*). Two of the genera—*Pelodera* Schneider, 1866 and *Rhabditis* (*sensu stricto*)—are subdivided into four and five subgenera respectively. One genus—*Brevibucca* Goodey, 1935—is accepted only provisionally in the Rhabditinae. The genus *Neorhabditis* Schuurmans Stekhoven, 1954 (syn. *Pararhabditis* Schuurmans Stekhoven, 1951; non Baylis and Daubney, 1926) is regarded as not belonging in the Rhabditinae.

In reviewing the names to be correctly applied to the nine taxonomic genera here recognized certain revisions have been made. The more important are the following.

The nominal genera *Ascaroides* Barthélemy, 1856, and *Leptodera* Dujardin [1844] (= *Agfa* Chitwood, 1935; non *Leptodera* Audinet-Serville, 1838), commonly treated as synonyms of *Rhabditis* (*sensu lato*), are determined not to be rhabditid at all. *Ascaroides* is probably a senior subjective synonym of *Cosmocercoides* Wilkie, 1930 (family Cosmocercidae, suborder Ascaridina). *Agfa* appears rhabditoid, but

fits none of the eight rhabditoid families; accordingly, a new family, Agfidae, is proposed for it.

The nominal subgenus *Curviditis* Dougherty, 1953, is now suppressed as a synonym of *Cephaloboides* Rahm, 1928, which is here retained in its original position as a subgenus in the genus *Rhabditis* (*sensu stricto*). The genus *Cuticularia* van der Linde, 1988, also falls as a synonym of *Cephaloboides*.

The genus *Epimenides* Gutiérrez, 1949, is a synonym of the subgenus *Cruznema* Artigas, 1927 (genus *Pelodera*).

The genus *Asymmetricus* Kreis, 1930 (syn. *Pseudorhabditis* Kreis, 1929, *non* Perroncito, 1880) is removed from candidacy as a name in the Rhabditinae by selection, as its type, of the cephalobid species, *Pseudorhabditis labiatus* [sic] Kreis, 1929, which belongs in the genus *Acrobeloides* Cobb, 1924—as *Acrobeloides labiatus* (Kreis, 1929) comb. nov.; *Asymmetricus* therefore falls as a synonym of *Acrobeloides*.

140 species are listed on pages 130-135 under the nine rhabditin genera, in the majority of cases without critical evaluation. 15 of these were not included by Osche (marked with an asterisk—*). Five names used by him are here changed (marked with a dagger—†). Many new combinations are established.

V. ADDENDA.

Since this paper was submitted to press, I have given further attention to a number of important points; works overlooked have come to my attention; and several significant papers have appeared. Accordingly a number of additional problems are taken up herewith.

1. The Composition of the Family Rhabditidae.

Although in the foregoing, main part of this paper the overall content of the family Rhabditidae has not been at issue, I have now decided to comment on it and make certain taxonomic proposals which are intended more to stimulate the constructive criticism and further work of other nematologists on the broader relations within the family and between it and other rhabditoid groups than to represent a definitive revision of the family.

As given by Chitwood (1950a, p. 12), the Rhabditidae consist of three subfamilies—Rhabditinae Micoletzky, 1922, Diploscapterinae

Micoletzky, 1922, and Bunonematinae (Micoletzky, 1922). The latter two groups are distinguished from the first by certain peculiar features—namely, by replacement of lips with hooks in the Diploscapterinae and by a highly ornamented cuticle and certain labial and cephalic characters in the Bunonematinae.

All of these groups share in common a relatively long, slender, cylindrical stoma, which terminates, in the case of the typical rhabditins, in a constricted section, the so-called "glottoid apparatus" (see Chitwood, 1950b, p. 67; also see next subsection for a discussion of the nomenclature of this structure). A glottoid apparatus is apparently absent in the diploscapterins (see Chitwood, 1950b, fig. 54E; also Goodey, 1951, pp. 19–20, fig. 7), but present as a typically constricted section in some at least of the bunonematins (as in *Bunonema stoeckherti* Sachs, 1949, fig. 5a) and as an apparently dilated, more weakly sclerotized section in others (see other figures of Sachs, 1949). Of the genera deriving from fragmentation of the genus *Rhabditis* (*sensu lato*) the glottoid apparatus is entirely lacking in *Protorhabditis* and *Parasitorhabditis*, and, in this, these thus resemble the diploscapterins. Osche regards them as primitive "subgenera" (see his proposed phylogeny as figured on p. 212 of his 1952 monograph); for a number of reasons his views on this matter of primitiveness seem well taken.

However, if one holds, as I feel is reasonable, that the nature of the bunonematin stoma suggests a close affinity between the bunonematins and the typical rhabditins, then it does not seem logical to exclude the former from the subfamily Rhabditinae, while at the same time including *Protorhabditis* and *Parasitorhabditis* therein. It would seem better either to eliminate certain subfamilial divisions in the Rhabditidae, or to effect further fragmentation. It is the latter course that I prefer.

It is now my feeling that the genus *Brevibucca* Goodey, 1935, is most appropriately placed in the family Rhabditidae. I further feel that two other genera—*Poikilolaimus* Fuchs, 1930, and *Rhabditonema* Körner, 1954—the first of these previously overlooked by me and the second only recently described, also can be placed in this family; the same may now be said for *Neorhabditis* Schuurmans Stekhoven, 1954. However, as to a fifth genus, another hitherto overlooked by me—*Macramphis* Altherr, 1950, which its author placed in the Rhabditidae, I am less sure. The question arises as to where in the family Rhabditidae these five genera should be placed. Coordinated with the answer to this problem, should be a decision as to the placement of *Protorhabditis* and *Parasitorhabditis*.

As I see the problem, there are three groups of genera in the Rhabditidae distinguishable on the basis of stomatal characters. One comprises the genera *Poikilolaimus* and *Brevibucca*, in which the stoma, though cylindrical, is broad and foreshortened and a glottoid apparatus is lacking; these, it may be remarked, tend to bridge the gap between the families Rhabditidae and Cephalobidae. The second comprises the diploscapterins and the genera *Protorhabditis*, *Parasitorhabditis*, and possibly *Neorhabditis*, which are characterized by a narrow, cylindrical stoma, but also lack a glottoid apparatus. And the third group comprises the typical rhabditins, plus the bunonematin, all with a relatively narrow, cylindrical stoma, characteristically terminated by a glottoid apparatus, or by a dilated area homologous to it and probably representing a secondary degeneration of the typical structure; this group also includes the genus *Rhabditonema*, the type species of which, *R. propinquum* Körner, 1954, has a glottoid apparatus.

Although Altherr (1950) described the type and only species of *Macramphis*, *M. stercoraria*, as having a *Rhabditis*-like stoma, the figure that he provided is by no means convincing of this. It does not appear to have a glottoid apparatus. I leave it here as *incertae sedis*.

I therefore suggest the following subfamilial division of the family Rhabditidae, based on the characters discussed:

1. Poikilolaiminae, subfam. nov. (type genus: *Poikilolaimus* Fuchs, 1930; other genus: *Brevibucca*).
2. Protorhabditinae, subfam. nov. (type genus: *Protorhabditis* (Osche, 1952) Dougherty, 1958; other genera (? 2): *Parasitorhabditis*, ? *Neorhabditis*).
3. Diploscapterinae Micoletzky, 1922 (type and only genus: *Diploscapter* Cobb, 1913).
4. Rhabditinae Micoletzky, 1922 (type genus: *Rhabditis* Dujardin [1844]; other genera (6): *Pelodera*, *Rhabditoides*, *Caenorhabditis*, *Mesorhabditis*, *Teratorhabditis*, *Rhabditonema*).
5. Bunonematinae (Micoletzky, 1922) (emended from Bunoneminae by Chitwood, 1935a; type and only genus: *Bunonema* Jägerskiöld, 1905—according to the revision of Sachs, 1949, although a less conservative treatment might well accord full generic status to the five subgenera recognized by him).
6. *Incertae sedis*: *Macramphis* Altherr, 1950.

The consequence of the foregoing is to modify the composition of the

subfamily Rhabditinae as presented in the main part of this paper by the elimination of two genera—plus *Brevibucca*, therein held uncertain as to affinities—and the addition of one genus, giving a net total of seven.

2. Nomenclature of the Rhabditoid Stoma.

Steiner (1933) introduced a system of terminology for the subdivisions of rhabditoid stomata, in which he made certain homologies for the typically rhabditids, the cylindrocorporids, and the cephalobids and later (1934) for the diplogasterids. This system has been followed by Chitwood (1950b) and Goodey (1951) in their nematode monographs and by Hyman (1951) in her treatise on the invertebrates, but unfortunately certain erroneous homologies are involved, already detected by Sachs (1950, p. 243), who has made modifications in the nomenclature of the rhabditid stoma such that in his scheme homologous rhabditoid parts bear the same names. He has been followed by Osche (1952), Körner (1954), and Skriabin *et al.* (1954) in their respective monographs. Nowhere, however, does the conflict in terminology appear to have been clearly perceived and enunciated.

Steiner (1933) applied the terminology in question fundamentally to the typical rhabditid stoma, in which he recognized a lip cavity, or *cheilostom*, a middle tube, or *protostom*, and an end structure (= glottoid apparatus), or *telostom*. In the genus *Cylindrogaster* Goodey, 1927 (*non* Stål, 1855 (Insecta); *nec* Rondani, 1856 (Insecta); *nec* Lioy, 1864 (Insecta); *nec* Fauvel, 1873 (Insecta); renamed *Cylindrocorpus* by Goodey, 1939) he recognized homologous sections, although the telostom therein was not in the form of a glottoid apparatus—in fact, he claimed that the telostom was “lacking,” but Goodey (1951) has described and figured a “telostom” with “knob-like” walls. When, however, Steiner arrived at the cephalobid stoma, which in some forms is characteristically and clearly divided into five successive cylindrical parts, each with separately sclerotized walls (see Sachs, 1950, fig. 2g), he made the error of assuming that the protostom of the rhabditid stoma was homologous with the middle three sections of the cephalobid stoma and the telostom of the former with the terminal segment of the latter; to the three middle sections of the latter he applied the terms *pro-*, *meso-*, and *metastom* and spoke of the *protostom* of the former as being fairly clearly divisible into a *prostom* and a *meso-metastom*, the latter of which, however, showed no clear subdivision into meso- and metastom. In extending this terminology to the diplogasterid stoma, Steiner (1934) recognized five sections with separately sclerotized walls

as in the cephalobids, although much modified in the former group into an overall funnel shape with large metastomatal teeth.

But the actual truth of the matter, as Sachs has shown, is that the rhabditid and cylindrocorporid "telostom," as the term was introduced by Steiner, is homologous with both the fourth ("metastom") and fifth ("telostom") sections of the cephalobid and diplogasterid stoma and that the fifth segment has as its counterpart in the rhabditids a narrow terminal ring at the base of the telostom (*sensu* Steiner) and is probably represented in the cylindrocorporids by the "knob-like" portion reported by Goodey. (Moreover, there appears from the latter's figure 10 to be a partially collapsed section just anterior to this in *Cylindrocorpus*, which probably is homologous with the rhabditid glottoid apparatus.) Sachs took the logical step of simply making such alterations as to render Steiner's nomenclature for the cephalobid pattern standard for the Rhabditoidea, thus changing the names of the more proximal parts of the rhabditid stoma. The terminologies of Steiner and Sachs, with correct homologies may be summarized as follows (with Steiner's cephalobid-diplogasterid nomenclature as the standard of reference and with the cylindrocorporid homologies left out because there remains an element of uncertainty in this last connection):

STOMATAL HOMOLOGIES.

| <i>Steiner's terminology as applied to the cephalobid and diplogasterid.</i> | <i>Steiner's terminology as applied to the rhabditid.</i> | <i>Sachs's terminology.</i> |
|--|---|-----------------------------|
| cheilostom | cheilostom | cheilostom |
| protostom | protostom + telostom (in part) | |
| prostom | prostom | prostom |
| mesostom | meso-metastom | mesostom |
| metastom | telostom (in part) | metastom |
| telostom | [unnamed; included in telostom] | telostom |

One might hold that since the initial application of Steiner's terminology was to the rhabditid stoma, one should, for reasons of priority of usage, adapt it to homologous structures of the cephalobid and diplogasterid, thus changing the names applying to the proximal parts of the latter and not *vice versa*. But it will be easily perceived that this would lead

to considerable confusion and that Sachs's solution is the better. The principal reason for reviewing this point here is to draw attention to the disagreement in usage between Steiner (and those who follow him) and Sachs (and those who follow him). Of particular importance is the fact that Steiner's usage has been incorporated into B. G. and M. B. Chitwood's monograph, *An Introduction to Nematology* (Chitwood, 1950b), which must be regarded at the present time as the standard treatise on nematode morphology and in which the term "telostom"—not "metastom," as in the usage of Sachs, Osche, and others—consistently refers to the glottoid apparatus of the rhabditid. Any departure from the Chitwoods' usage should be carefully explained; and this is what I have attempted to do here.

8. Miscellanea.

There are a few additional points to be made.

Li (1951) has described tentatively as new a species, *Rhabditella multipara*. Osche (*in litt.*) identifies this with what I here call *Rhabditis* (*Rhabditella*) *axei* (Cobbold, 1884) comb. nov.

Skriabin *et al.* (1954) have published the fourth and final volume of the monumental Russian treatise, *Opredelitel' Paraziticheskikh Nematod*, in which the rhabditids are treated. The Soviet workers recognize *Rhabditis*, *Brevibucca*, *Parasitorhabditis*, *Rhabditella*, and *Rhabditoides* as genera of the subfamily Rhabditinae, thus largely following Chitwood (1950a). Osche's reforms are therefore essentially ignored despite the fact that his monograph is cited. They list 28 named species (plus one variety and 3 unnamed species) of *Rhabditis*, 12 "species" of *Parasitorhabditis* (thereby raising the varieties of Fuchs, 1915, 1937, to specific rank), and three species of *Rhabditella* as occurring as parasites of animals. Under *Rhabditis* are listed two forms not hitherto reviewed by Osche or by me—*Rhabditis erschowi* Abuladze, 1934, and *Rhabditis terricola spiculofusum* Abuladze, 1934. Osche (*in litt.*) reports that he regards *R. teres spiculofusum* as *R. terricola*, and *R. erschowi* as a good species, falling in his "longicaudata-group". I would therefore call the latter *Rhabditis* (*Choriorhabditis*) *erschowi* Abuladze, 1934; it represents a 24th species in the subgenus *Choriorhabditis*.

Meyl (1954) has published a monograph on Italian soil and freshwater nematodes. He states therein that in his opinion *Rhabditis* (*Choriorhabditis*) *demani* Hnatewytsh, 1929, is not the same as *Rhabditis oxycerca*, de Man, 1895—in disagreement with Osche's

decision that this is so. (However, after visiting Osche, Meyl (*in litt.*) now agrees with him.) Also, he describes a new species, *Rhabditis resistens*, which he regards as unallocatable as to subgenus (in Osche's system) for want of male specimens. Actually this alone need not entirely prevent its allocation. It may be noted that the constellation of characters given by Meyl would locate it in Osche's *Choriorhabditis* except for its lack of an esophageal "sleeve" projecting forward about the base of the stoma. I should, nevertheless, tentatively refer it to the genus *Rhabditis* here, but cannot allocate it as to subgenus.

Osche (1954b) has reported a very interesting study on a number of groups of twin and complementary rhabditid species. He now agrees—at least provisionally—to the separation of what I now call *Caenorhabditis clavopapillata* and *C. briggsae* as independent species.

According to a paper by Rühm (1954) a monograph by him, which will doubtless include his revision of the genus *Parasitorhabditis*, is in press.³⁴ He recognizes this genus as independent of *Rhabditis*.

In conclusion, it now becomes necessary to emend the statements in the SUMMARY of the main part of this paper to the effect that I recognize nine genera and 140 species in the subfamily Rhabditinae. With the elimination of *Protorhabditis* (12 species), *Parasitorhabditis* (two species), and *Brevibucca* (two species) and with the addition of *Rhabditonema* (one species) and two species of *Rhabditis* created by Abuladze and by Meyl respectively, there are now left seven genera and 127 species in the subfamily.

³⁴ "Die Nematoden als Kommensalen, Halbparasiten und Parasiten der Insekten. Vortrag am Deutschen Entomologtag Hamburg 1953."

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³⁵ These include citations to all papers in which appeared (1) the naming of nematode species and genera listed herein, (2) the first use of combinations of generic and specific names, and (3) the first use of names of higher categories (families, etc.) of nematode groups; but do not include citations to papers in which first appeared the names of cited host organisms. All references listed here have been consulted in the original, or in photocopy thereof.

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Further Observations on the Occurrence of Nematodes of the Genus *Meloidogyne* in the Gold Coast

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In a recent publication, the writer (Edwards, 1953) recorded the presence of the root-knot nematode for the first time in the Gold Coast. It was revealed that it had been found in all stages of development on eleven species of cultivated plants and that during a search to discover the source of the infestation it was detected on three indigenous wild hosts. In the course of more intensified studies subsequently made, many additional host plants, both cultivated and wild, suitable for the maintenance and multiplication of the parasite have been discovered.

LIST OF HOST PLANTS.

The plants found hitherto attacked by root-knot nematodes in the Gold Coast, based on field observations and laboratory confirmations, by the writer, include :—

- AMARANTACEAE : *Amaranthus spinosus* Linn. (A weed).
 Celosia argentea Linn. (A weed).
 Gomphrena globosa Linn. (Cultivated flower).
BALSAMINACEAE : *Impatiens balsamina* Linn. (Balsam).
BASELLACEAE : *Basella alba* Linn. (Creeping spinach).
BROMELIACEAE : *Ananas sativus* Schult. (Pine-apple).
CAPPARIDACEAE : *Cleome ciliata* Schum. and Thonn. (Wild spinach).
CARICACEAE : *Carica papaya* Linn. (Pawpaw).
CHENOPODIACEAE : *Beta vulgaris* Linn. (Garden beet).
 Spinacia oleracea Linn. (Common spinach).
COMPOSITAE : *Ageratum conyzoides* Linn. (A weed).
 Lactuca sativa Linn. (Lettuce).
 Melanthera brownei Schuktz. (A weed).
 Helianthus annuus Linn. (Sunflower).
 Zinnia elegans Jasq. (Common zinnia).

- COMMELINACEAE : *Commelina lagosensis* C.B. Cl. (A weed).
- CONVOLVULACEAE : *Ipomoea batatas* Lam. (Sweet potato).
Ipomoea cairica Sweet. (A weed).
Ipomoea digitata Linn. (A weed).
- CRUCIFERAE : *Brassica napus* Linn. var. *napabrassica* . (Swede).
Brassica oleracea Linn. var. *gongyloides* (Kohl rabi).
Brassica oleracea Linn. var. *capitata*. (Cabbage).
Brassica oleracea botrytis Linn. var. *cauliflora* (Cauliflower).
Brassica pekinensis Skeels. (Wongbok or Chinese cabbage).
Brassica rapa Linn. var. *rapa*. (Cattle turnip).
- CUCURBITACEAE : *Citrullus vulgaris* Schrad. (Water melon).
Cucumis melo Linn. (Sweet melon).
Cucumis sativus Linn. (Cucumber).
Cucurbita pepo Linn. (Pumpkin).
- EUPHORBIACEAE : *Acalypha ciliata* Forsk. (A weed).
Euphorbia heterophylla Linn. (A weed).
Euphorbia prostrata Ait. (A weed).
Manihot utilissima Pohl. (Cassava).
- FICOIDACEAE : *Trianthema portulacastrum* Linn. (A weed).
- GRAMINEAE : *Brachiaria deflexa* Hubbard. (Grass).
Panicum maximum Jacq. (Guinea grass).
Saccharum officinarum Linn. (Sugarcane).
Setaria barbata (Lam.) Kunth. (Grass).
Sorghum arundinaceum (Desv.) Stapf. (Grass).
Sorghum vulgare Pers. (Guinea corn).
- LABIATAE : *Mentha viridis* Linn. (Mint).
Solenostemon occymoides Schum. & Thonn. (A weed).
- LILIACEAE : *Allium cepa* Linn. (Onion).
Asparagus officinalis Linn. (Asparagus).
- MALVACEAE : *Abutilon* sp. (A weed).
Hibiscus esculentus Linn. (Okra).
Hibiscus sabdariffa Linn. (Roselle).
Hibiscus vitifolius Linn. (A weed).
- MUSACEAE : *Musa sapientium* Linn. (Banana).
- PALMAE : *Elaeis guineensis* Jacq. (Oil palm).

- PAPILIONACEAE : *Cajanus indicus* Spreng. (Pigeon pea).
Clitoria ternatea Linn. (Blue pea).
Canavalia ensiformis DC. (Canavalia bean).
Mucuna atterima Comb. Nov. (Bengal bean).
Phaseolus aureus Roxb. (Cultivated legume).
Phaseolus multiflorus Willd. (Runner bean).
Phaseolus semi-erectus Linn. (Cultivated bean).
Phaseolus vulgaris Linn. var. *humilis*. (Dwarf bean).
Vigna unguiculata Walp. (Cow pea).
- PEDALIACEAE : *Ceratotheca sesamoides* Endl. (A weed).
- PORTULACACEAE : *Portulaca oleracea* Linn. (A weed).
Portulaca quadrifida Linn. (A weed).
Talinum triangulare Willd. (Wild spinach).
- SOLANACEAE : *Capsicum annuum* Linn. (Red pepper).
Lycopersicum esculentum Mill. (Tomato).
Nicotiana tabacum Linn. (Tobacco).
Petunia violacea Lindl. (Cultivated petunia).
Physalis angulata Linn. (A weed).
Solanum melongena Linn. (Eggplant).
- STERCULIACEAE : *Theobroma cacao* Linn. (Cocoa).
- TILIACEAE : *Corchorus tridens* Linn. (A weed).
Corchorus olitorius Linn. (Jute).
- UMBELLIFERAE : *Daucus carota* Linn. (Carrot).
Petroselinum sativum Hoffm. (Parsley).
- VERBENACEAE : *Clerodendron scandens* Beauv. (A weed).
- VIOLACEAE : *Viola odorata* Linn. (Sweet violet).

REACTIONS OF HOSTS.

These seventy-six plant species showed marked differences in their reactions to infestations. The galls on the roots of some host plants were always small, while in others the entire root system had become a distorted, twisted, swollen mass, virtually useless to the plant. Out of the seventy-six species of plants found attacked, approximately a third of them are common, indigenous weeds in the Gold Coast. Although the weeds exhibited appreciable variations in their degree of susceptibility to the parasites, none of them could be regarded as severely attacked, judging by the number and size of the galls on their roots.

All the circumstantial evidence points to the conclusion that the root-knot eelworm is long established in the Gold Coast and that there is a state of equilibrium between it and its wild hosts. Some plant species which have been cultivated in the territory for a very long time, such as *Manihot utilissima* (cassava), *Hibiscus sabdariffa* (roselle) and *Capsicum annum* (red pepper), are also able to withstand attacks and remain comparatively free of root distortion or galls due to the presence of the parasite. Other cultivated plant species introduced in the last quarter of a century, such as tomatoes, cucumber, melon, onion, carrot, lettuce, spinach and brassicae of various kinds, are liable to develop extreme root manifestations characteristic of serious attacks by the root-knot nematode. Some species of cultivated plants for example, *Brassica oleracea capitata* and *cauliflora* (cabbage and cauliflower) and *Lactuca sativa* (lettuce) are tolerant of fairly heavy infestations while others such as *Phaseolus multiflorus* and *P. humilis* (beans), *Beta vulgaris* (garden beet) and *Lycopersicum esculentum* (tomato) succumb to a comparatively small number of nematodes.

AMARANTACEAE.

The three host plants belonging to this family, *Amaranthus spinosus*, *Celosia argentea* and *Gomphrena globosa*, are highly attractive to the root-knot nematode in the Gold Coast but none of them display any symptoms of attack apart from the presence of galls on their roots. *A. spinosus* and *C. argentea* are exceedingly common weeds, particularly on land under arable condition, but the galls on their roots are seldom very numerous, each being usually in the form of a slightly widened, oval area of the root. The other host plant, *G. globosa*, which is often grown in flower borders and in rock-gardens in the southern region of the Gold Coast, is subject to much heavier infestations. The galls are abundant and irregular in shape, some often attaining the size of broad-bean seeds.

BALSAMINACEAE.

The garden balsam, *Impatiens balsamina*, produces wonderful display of bloom over the greater part of the year along the southern fringe of the Gold Coast but it is particularly liable to serious attacks of the root-knot eelworm. Affected plants normally survive, however, under good growing conditions, to produce a wealth of bloom, though their roots may be a mass of distorted, swollen structures.

BASELLACEAE.

The perpetual, creeping form of spinach, *Basella alba*, introduced into the Gold Coast some thirty years ago and widely grown in most parts of this territory produces an enormous yield of succulent foliage throughout the year. It is highly attractive to the root-knot nematode and its roots in time develop into twisted, swollen structures. The new roots which are being continuously formed at intervals by the shoots creeping over the ground remain comparatively free of serious manifestations while spreading near the surface of the soil but eventually on penetrating into deeper layers they become severely galled. The degree of attack, judging by manifestations shown by the roots, varies immensely in different parts of the Gold Coast, being particularly severe in crops grown in the alluvial soils alongside the Volta River.

BROMELIACEAE.

New plantations of pine apple, *Ananas sativus*, are being established at a rapid rate in the Gold Coast to meet the increased demand for the fruit of this plant. Hitherto, this comparatively new enterprise has proved a great success and it is proposed to plant shortly, under the auspices of the Gold Coast Agricultural and Fisheries Development Corporation, areas of many thousands of acres for the canning industry and export trade. A special search for the root-knot eelworm recently made by the writer in existing pine-apple plantations has revealed that the parasite has already established itself on this plant in some localities in the Gold Coast. It was evident that, although the degree of infection in all cases was low, the nematode had been able to support itself and multiply freely on the roots. Most of the affected plants had an enormous mass of roots, none of them being long but each having branched and sub-branched to form a dense aggregation of short-stunted rootlets. On the young, delicate rootlets, small galls occurred with adult females, ova and larvae of the root-knot nematode in them in appreciable numbers.

CAPPARIDACEAE.

The wild spinach, *Cleome filata*, is a weed which grows very rapidly and flourishes well in a variety of habitats in the Gold Coast. Although it constitutes one of the most important wild hosts for the maintenance of the root-knot eelworm, particularly on land kept under cultivation, the galls on its roots are always small in size and comparatively few in number.

CARICACEAE.

Various varieties of pawpaw, *Carica papaya*, are extensively grown over the greater part of the Gold Coast except in the dry savannah regions of the north and the dry Accra plains along the coast in the south. They are not grown in large plantations but as isolated trees around the homesteads and among the fruit, vegetable and herbage crops. The galls set up on their roots due to the presence of the root-knot nematode are numerous but relatively small in size. No distinctive symptoms of attack are shown by the aerial parts of the affected trees. Obviously, the common practice of growing pawpaw trees for their fruit, indiscriminately among all kinds of crops rather than in definite plantations is a method which should be discouraged in order to minimise the ravages caused by the root-knot eelworm to other cultivated plant species.

CHENOPODIACEAE.

The two species in this family, the garden beetroot, *Beta vulgaris*, and the European spinach, *Spinacia oleracea*, are attacked in the Gold Coast by the root-knot eelworm. In each case, the roots are malformed into large irregular galled masses, and of the two species, garden beetroot is the more seriously affected.

COMPOSITAE.

Judging from the severe degree of galling of the roots of lettuce, *Lactuca sativa*, sunflower, *Helianthus annuus*, common zinnia, *Zinnia elegans*, and the two common weeds, *Ageratum conyzoides* and *Melanthera brownei*, it would seem that plant species belonging to the *Compositae* are highly attractive to the root-knot eelworm in the Gold Coast. Although the roots often become seriously deformed, other organs usually continue to make satisfactory growth and show no marked indications that they are deprived of their normal nutriment until the plant has attained full maturity. In contrast to lettuce and zinnia, the other three species though subject to attack seldom develop large compound galls on the roots. It would appear that the roots of the sunflowers and the two weeds are equally as attractive to the root-knot nematode as those of the lettuce and zinnia, judging by the number of galls, but that the presence of the parasite does not stimulate such marked gall formation on them.

It is also noteworthy that a striking difference in the degree of infestation of the wild host, *A. conyzoides*, was discerned at one centre

where intensive field observations were made on the reactions of different plant species to attack. Plants which had established themselves between the roots of badly affected carrots were very heavily infested compared with those growing on the headlands and on the adjoining uncultivated ground. The parcel of land with the carrots had only recently been converted from its wild state into a suitable condition for arable cropping and the carrots constituted the first arable crop grown on it. Was this marked variation in the degree of infestation of the roots of the weed *A. conyzoides* by the root-knot eelworm due to influence produced by the roots of the carrot plant? Had the root secretions of the carrots stimulated greater hatching of the larvae from the ova present in the soil than those of *A. conyzoides*?

COMMELINACEAE.

The wild host plant, *Commelina lagosensis*, is a common host of the root-knot nematode in many areas in the Gold Coast. Although its roots prove highly attractive to this parasite, the galls always remain small in size.

CONVOLVULACEAE.

In this family, the cultivated sweet potato, *Ipomoea batatas*, and the two weeds, *I. cairica* and *I. digitata*, are exceedingly common hosts of the root-knot eelworm in the Gold Coast. When cultivated sweet potato crops are attacked by this nematode, the yields are invariably poor and, in extreme instances, tuber formation is virtually inhibited and all the finer roots showing a marked knotted appearance. Of these three host plants, the climbing, clinging weed, *I. cairica*, usually exhibits the least root reactions to the nematode, the galls being comparatively smaller in size and fewer in number. The bush or wild sweet potato, *I. digitata*, flourishes well everywhere even under the most dry soil and climatic conditions, the enormously developed tubers enabling the plant to stand severe droughts over long periods. Although its roots become appreciably galled when attacked by the eelworm, the infection rarely leads to any adverse effects detectable on examination of the foliage. Seldom any attempt is made to destroy this weed because the contents of its tubers form the basis of several concoctions used by Africans for curing various kinds of pains and skin diseases. It, therefore, constitutes an important reservoir for the root-knot eelworm in West Africa since it plays such a significant part in native medicine and can survive under extraordinarily varied soil and atmospheric conditions.

CRUCIFERAE.

All the cruciferous plants hitherto found infected by the root-knot nematode in the Gold Coast belong to the genus *Brassica*. They consist of cabbages, cauliflowers, Wongbok (Chinese cabbages), Kohl rabi, swedes and turnips, all being cultivated plants grown on an increasing scale, in acreage and distribution, from seed imported for the purpose each year from South Africa, United Kingdom and America. The total acreage grown is still very small, amounting in no locality to more than a few acres due not to the ravages of the root-knot eelworm or any other parasite but rather to lack of suitable varieties for the peculiar environmental conditions of the Gold Coast. All these host plants are subject to varying degree of distortion of their roots due to presence of the nematode but rarely any of them succumb to attack before attaining full growth except when grown in soils of exceptionally heavy infestation lacking in satisfactory conditions for plant development.

CUCURBITACEAE.

Of all the plant species hitherto recorded as hosts of the root-knot nematode in the Gold Coast, none exhibit more severe reactions to the presence of this parasite than the water melon, *Citrullus vulgaris*, sweet melon, *Cucumis melo*, cucumber, *C. sativus*, and pumpkin, *Cucurbita pepo*. When grown on infested land, their roots soon develop into badly swollen, distorted structures useless to maintain normal growth and the plants die at an early stage, often before the production of any fruit.

EUPHORBIACEAE.

Judging from the infestations of the root-knot eelworm on the roots of the cassava, *Manihot utilissima*, and the three common weeds, *Acalypha ciliata*, *Euphorbia heterophylla* and *E. prostrata*, it would appear that the plant species belonging to the Euphorbiaceae are highly attractive to this parasite in the Gold Coast. They seldom show, however, serious malformations of their root systems or any adverse effects in their aerial parts even in the case of the cultivated cassava. The galls are often numerous and although they usually remain small in size the nematodes multiply freely in them. The three weeds, particularly *A. ciliata* and *E. heterophylla*, serve as extremely important wild reservoir-hosts since they quickly establish themselves among cultivated plants.

The cassava plays an equally significant part in the maintenance of the root-knot nematode on infested land and even a greater part in its dissemination into new areas. The cassava forms a staple diet of the people over most of the Gold Coast and it is grown in small areas everywhere as soon as the virgin forest is cleared except in places where yam can be successfully cultivated instead of it. The cassava can thrive even on exceedingly poor soils and in regions subject to long periods of drought. It needs hardly any attention and it can be left growing in the ground, unless its tubers are required, for several years. The root-knot eelworm readily establishes itself on cassava, particularly in the fine rootlets at the junction of the stem and its underground swollen stolons which ultimately develop into the tubers used for human consumption.

FICOIDACEAE.

The weed, *Trianthema portulacastrum*, observed as a host plant of the root-knot nematode in the Gold Coast acts undoubtedly as one of the most prevalent reservoir hosts over extensive regions of this colony. Besides being a common weed of waste places it soon establishes itself on land brought under cultivation for arable cropping. It is often found infested when growing on land still in its natural condition and an appreciable distance from any cultivated areas. The galls set up on the roots are fairly numerous but, like those formed on most wild host plants, they never develop into large compound structures.

GRAMINEAE.

Of the large number of species of Gramineae examined by the writer from time to time in the Gold Coast, only six species have been noted with galls on their roots due to the presence of the root-knot eelworm. In the case of Guinea corn, *Sorghum vulgare*, and the four grasses, *Brachiaria deflexa*, *Panicum maximum*, *Setaria barbata* and *Sorghum arundinaceum*, the galls are very few in number and small in size, each normally containing only a single female worm. They are globular to oval in shape and often either showing signs of bursting or having burst through the tissues of the root and revealing masses of ova around the vulva of the female. Of these five species, it would seem that *B. deflexa* is by far the most attractive to the nematode or at least offers the least resistance to the parasite establishing itself and reproducing within its tissues, judging from

the results of the counts made of the number of galls present on their roots. How widely distributed is this nematode on sugar cane, *Saccharum officinarum*, in the Gold Coast is not known but at two centres, Nsawam and Pokoasi, where it is grown on a small scale, high proportions of the finer roots are beset with small, irregular shaped galls containing the parasite in all stages of development from egg to adult.

LABIATAE.

In a private garden at Tarkwa in the Western Province of the Gold Coast, the roots of mint, *Mentha viridis*, were found lightly infested by the root-knot eelworm, the galls being very few in number and only just visible to the unaided-eye. All stages of the parasite occurred in them. In the same garden, the weed, *Solenostemon ocymoides*, was also infected by this nematode and to a much heavier degree, the galls being more numerous and greater in dimensions.

LILIACEAE.

In the Liliaceae, both the asparagus, *Asparagus officinalis*, and the onion, *Allium cepa*, suffer severely from depredations of the root-knot nematode in the Gold Coast, when grown even on lightly infested land. At first, the onions make a satisfactory progress but whilst still in the seedling stage they suddenly cease to grow and then slowly die. An affected plant shows a general widening of its individual roots, usually in areas of $\frac{1}{2}$ -1 $\frac{1}{2}$ inches here and there along their entire length. The larvae which hatch from eggs laid in these thickened parts travel freely in the root tissues to set up new centres of infection.

The malformations on the roots of the asparagus assume the typical gall-like swellings and distortions normally associated with the root-knot eelworm. As a rule, once asparagus plants establish themselves, they can withstand heavy attacks but rarely produce economical returns for the grower.

MALVACEAE.

Four species of the Malvaceae act as important host plants in the perpetuation and dissemination of the root-knot nematode in the Gold Coast. Two of them are cultivated species, the okra, *Hibiscus esculentus*, and the roselle, *H. sabdariffa*, while the other two species

constitute common and troublesome weeds, *H. vitifolius* and *Abutilon* sp. The okra has been cultivated from a very early period by Africans in the Gold Coast for its fruit, and a few bushes are grown today by almost every holder of land in most regions. It is highly attractive to the root-knot eelworm and although large compound galls often develop on its roots the yield of fruit is seldom adversely affected.

The roselle, also called Red or Indian sorrel, in common with okra, has been cultivated from time immemorial in the Gold Coast. Most families with suitable land at their disposal grow a few plants of this herb for their leaves and fruit capsules which are considered valuable ingredients in soups. Like the okra, the root system of the roselle proves a useful medium to the root-knot nematode for its substance and multiplication. The galls set up by the parasite on the finer roots consist of small, oval swellings, while on the old roots, the majority of them take the form of elongated, blister-like, cankerous outgrowths, usually widely separated and causing little or no obvious detriment to the plant.

The weed belonging to the genus *Abutilon* also serves an extremely valuable host plant to the parasite in the Gold Coast, partly on account of the fact that this prevalent perennial plant of the "bush" and waste places is extensively used in the form of water infusion of its foliage for the treatment of haematuria. Consequently, it is allowed to grow even on cultivated land thereby enabling the nematode to bridge the period when suitable food is not available for it. This weed can maintain itself under extremely adverse conditions of drought by drawing on the carbohydrates and other nutrients stored in its large, underground tubers. The galls occur in considerable numbers on the finer roots but they almost invariably remain quite small and there is no evidence that the other organs of the plant suffer in any way from the infestation. The infection in the other wild host, *Hibiscus vitifolius*, results in an appreciable amount of knotting of its roots. It is a weed that quickly establishes itself among cultivated plants in many areas in the Gold Coast and in its galled tissues the parasite often occurs extraordinarily abundant.

MUSACEAE.

The banana, *Musa sapientum*, is the only species of this family found infested by the root-knot eelworm in the Gold Coast. At the two centres, Pokoasi and Dabri, where it occurs on the banana, no

obvious indications of its presence are displayed by the aerial parts, and normal egg-laying females are quite rare in the woody galls formed on the roots. It would seem that there is an incompatibility between the host and parasite, which is, at least, detrimental to the latter.

PALMAE.

The palm tree, *Elaeis guineensis*, highly valued by the Africans in West Africa for its oil and wine often harbours light populations of the root-knot nematode in all phases of development. There are seldom easily recognised galls, however, present on the root system but rather abnormal conformations of the individual roots, in the slightly swollen parts of which the parasite occurs.

PAPILIONACEAE.

Judging from the degree of infestations of the root-knot eelworm observed on the roots of the blue pea, *Clitoria ternatea*, cowpea, *Vigna unguiculata*, pigeon pea, *Cajanus indicus*, dwarf bean, *Phaseolus vulgaris* var. *humilis*, runner bean, *P. multiflorus*, sword bean, *Canavalia ensiformis*, Bengal bean, *Mucana aterrima*, and the beans *Phaseolus semi-erectus* and *P. aureus*, it is apparent that plant species of the family Papilionaceae are highly attractive to this parasite in the Gold Coast.

The blue-flowered, climbing bean and prolific grower, *C. ternatea*, which is commonly grown in many parts of West Africa to adorn buildings and provide shade from the tropical sun is almost everywhere, at least, in the Gold Coast attacked by the root-knot nematode. Once the plants become well established, the roots continue to grow at an exceedingly rapid rate just beneath the surface of the soil and downwards to considerable depths. At first, gall formation proceeds very slowly but ultimately, under the influence of the secretions of generations of the parasite, the older roots develop into massive deformed structures. There is no evidence that this abnormal development, however, leads to any form of crisis in the metabolism of the plant. This blue pea is sometimes grown by farmers either for its fodder or seed but it is rarely left long enough in the ground for the roots to become seriously galled.

The cowpea now extensively grown in the Gold Coast was introduced into the colony some two or three decades ago from Atakpame, a town in French Togoland in West Africa. It is often

claimed that this cowpea is immune to attacks by the root-knot eelworm since it produces good yields of pods full of white to cream coloured seeds on land where most other crops fail due to the ravages of this pest. It is evident from the results of extensive tests conducted by the writer that the plant is subject to heavy invasions by the larvae and that no profound changes are stimulated during early stages of parasitism in the morphology and physiology of the surrounding plant tissues. Even under these circumstances the larvae are able to develop to maturity and result in further generations within the root tissues. No doubt, the extraordinarily rapid growth of this blue pea, being able to reach full maturity within eight weeks of sowing the seed, plays an important part in the apparent resistance to attack based on general vigour of foliage and yield of seed.

The pigeon pea commonly cultivated in the Gold Coast also shows resistance to the detrimental influences which usually follow invasions of the root tissues by the parasite, judging by the extent of foliage and yield of seed given by it on infested land when compared with the production of plant species highly susceptible to injury from its depredations, such as dwarf and runner beans. In contrast to the blue pea and cowpea, the pigeon pea is not capable of withstanding heavy attacks and its roots become obviously galled at a fairly early stage of parasitism.

Both the dwarf and runner beans, on the other hand, suffer severely even when grown on land of comparatively light infestations. At first these plants grow quite normally but after reaching a good size they suddenly collapse and die, usually in the early flowering stage and before any seed is set. At an early phase of parasitism, the entire root system becomes malformed into enlarged nodular and twisted structures which soon afterwards, largely due to secondary invasion of other organisms, break down and decay. It would seem that the resistance to ill effects of the parasite breaks down at a very early stage of parasitism in the dwarf and runner beans whilst in the blue pea it remains at a high level throughout the life of the plant. The pigeon pea and the cowpea are intermediate in this respect, the former being decidedly less resistant than the latter.

It would appear that in the other two species of the genus *Phaseolus* there is an incompatibility between the host and parasite which is detrimental to a marked extent to both. They do permit just enough female worms to attain maturity and lay sufficient eggs

to supply a continuing source of infective larvae. The plants themselves do not escape injury. Small galls occur singly and sparsely and when the roots are invaded by larvae in appreciable numbers a high proportion of the root tips are killed and new rootlets develop to compensate for them. This results in excessive branching and development of short, stunted rootlets and in turn, often retardation in growth of the plant.

Observations have only been made by the writer at one centre in the Gold Coast on the susceptibility of Bengal and Canavalia beans to attack by the root-knot eelworm. At the time of inspection, the plants had reached the half-grown stage and were growing vigorously. A light population of the parasite in all its stages was present and relatively few galls had been formed.

PEDALIACEAE.

The species, *Ceratotheca sesamoides*, which proves a troublesome weed of cultivated land in places in the Gold Coast is liable to attacks by the root-knot nematode. Its roots become slightly galled and there is a tendency for excessive development of short, stunted rootlets.

PORTULACACEAE.

The three species of the Portulacaceae, *Talium triangulare*, *Portulaca quadrifida* and *P. oleracea*, which harbour the root-knot eelworm in the Gold Coast, are extremely prevalent weeds of cultivated land in many areas of West Africa. *T. triangulare*, regarded in the Gold Coast as the wild indigenous spinach, is a favoured plant in many parts since its foliage contributes to the local diet. The parasites readily enter its root tissues where they soon build up into heavy infestations and result in the rapid production of multinucleated giant-cells which lead to unusually large gall-formations for a wild host. *T. quadrifida* forms a low, dense covering over the ground and on its roots, when the plant is growing on infested land, abnormally large, roughly globular galls soon make their appearance. They are very few in number and often grow to the size of a bean-seed or even a hazel-nut which is remarkable for a plant with fine, hair-like roots. At first, the galls are comparatively soft in texture but later develop into rather hard woody structures, in most of which no parasite can be found. The exact relationship between the parasite and this unusual gall-formation is not known and it has been made the subject of a further investigation. *P. oleracea* is much less liable to infection

than the other two species and the galls remain insignificant, each being merely a slight, oval enlargement of the root itself. The number of affected plants is always low and the parasites, when present, are never plentiful.

SOLANACEAE.

The six cultivated species of Solanaceae, tomato, *Lycopersicum esculentum*, red pepper, *Capsicum annum*, egg-plant, *Solanum melongena*, tobacco, *Nicotiana tabacum*, petunia, *Petunia violacea* and the weed *Physalis angulata*, which are known as host plants of the root-knot nematode in the Gold Coast, show marked pathological reactions to the presence of the parasite in their roots. Of all these species, the tomato suffers by far the most injury and it can be classified in this respect with cucumbers, melons, dwarf and runner beans. Attacked tomato plants even when grown on lightly infested land fail to produce any marketable fruit and the plants remain spindly and yellowish green in colour and they readily wilt in dry weather. When grown on moderately to severely affected ground, they are killed outright while still quite young and before any fruit trusses are formed. Profound pathological changes take place in the root tissues soon after their invasion by the parasite in appreciable numbers and all the roots develop into badly swollen, deformed structures. This phase is quickly followed by a subsequent breakdown and decay of the entire root system, largely caused by the secondary invasion of other organisms.

Although the red pepper and the egg-plant are also highly attractive to the parasite and liable to a marked gall-formation on their roots, they do not suffer to the same extent as the tomato plant. The galling on their roots is less pronounced and the subsequent breakdown and rotting of the root system develop only under rare circumstances. Even when grown on land where the tomato crop is a complete failure, both the red pepper and egg-plant continue to make good growth of foliage and produce fruit but on a reduced scale compared with plants on non-infested ground. The tobacco in its degree of susceptibility to severe galling of its roots and pathological manifestations in its aerial parts is intermediate in this respect between the tomato and the red pepper or egg-plant.

The cultivated petunia produces exceedingly good bloom in the Gold Coast and by repeated sowings and transplantings, a succession of excellent displays can be ensured throughout the whole year.

Unfortunately, the petunia is very attractive to the root-knot eelworm and under this system of intensive cropping, heavy infestations of the soil are soon built up. At first when grown in areas of moderately heavy infestations, petunias make good growth but soon after reaching the flowering stage they readily wilt and the foliage becomes yellow, brown and dead. Gall-formation develops at an early stage of parasitism and soon it involves a high proportion of the root system.

The wild host, *Physalis angulata*, frequently referred to locally in the Gold Coast as the African gooseberry, is often found lightly infested by all stages of the root-knot eelworm in its roots, at least, when growing on cultivated land among affected crops. Apart from the presence of a relatively few, small galls on the root system, no other pathological manifestation is discernible.

STERCULIACEAE.

The entire economy of the Gold Coast virtually depends on the production of cocoa beans for export purposes and among the various pests which attack the cocoa tree, *Theobroma cacao*, is the root-knot eelworm. Seedlings raised in infested soil frequently have galls on their roots due to this parasite but these galls always remain fairly small and the infestation usually tends to die out unless other more suitable hosts growing in the immediate vicinity continue to provide new larvae to start fresh foci of infection on the young developing rootlets.

TILIACEAE.

Galls due to the presence of the root-knot nematode in the root tissues sometimes occur on jute, *Corchorus olitorius*, and the weed, *C. tridens*, but they never assume such proportions as to affect the general health of these plant species. As the jute grows, the galls develop into hard, woody structures, in most of which no live nematodes can be discovered, although occasionally it is possible to recover a dead parasite.

UMBELLIFERAE.

Two cultivated species of Umbelliferae introduced in recent years into the Gold Coast, the carrot, *Daucus carota*, and parsley, *Petroselinum sativum*, are usually complete failures when sown on land harbouring the root-knot eelworm. Carrots, when grown on heavily infested land, make at first a satisfactory growth but within a month when the

roots are about $\frac{1}{4}$ inch in maximum diameter, the plants suddenly stop growing and the foliage soon turns brown and dies. Shortly before stagnation of growth manifests itself, almost the entire root system becomes seriously galled and as fast as new rootlets are formed to replace those virtually rendered useless they too become studded with egg-laying females and valueless to the plant. On lightly infested land, the carrots may withstand the attack and produce roots just large enough for human consumption. Even in such cases, the finer roots are badly galled but, in contrast to the tomato, cucumber, melon, dwarf and runner beans, this pathological condition is not followed by a breakdown and decay of the entire root system. It is noteworthy in this connection that on careful examination of the so-called "main root," that is, the part used for human consumption, it is usually found that the surface is thickly beset with small wart-like, succulent outgrowths, often barely visible to the naked eye. Each protuberance is composed of an aggregation of thin-walled cells either around or in the immediate vicinity of a lenticel. It would seem that the plant tissue in these outgrowths are in such a condition that they provide a most useful source of food for the requirements of the nematode, judging by the numbers of all its stages present in them.

The parsley definitely suffers less than the carrot from the harmful influences resulting from attacks by this parasite. Gall formation is never such a prominent feature and the infection always leads to excessive development of very much branched root system reminiscent in many respects of the conditions produced in sugar-beet and other plants when attacked by nematodes of the genus *Heterodera*. When the root tip is invaded by an appreciable number of larvae, the growing point is destroyed and the root then branches. These branches in turn are attacked and sub-branch and the process continues until ultimately the entire root system becomes most abnormal in conformation.

VERBENACEAE.

An exceptionally deep rooted species, *Clerodendron scandens*, belonging to this family is, in the Gold Coast, often a host plant of the root-knot eelworm even when growing on land still in its primitive, natural condition. It is an extremely common species over extensive areas in this colony and its eradication remains a most difficult problem for several years after the land has been brought under cultivation. Although the galls are always small and very sparse in their occurrence

on the roots, there are no indications that the tissues at the region of invasion respond so slowly that the nematode develops and multiplies under stunting influence of its host.

VIOLACEAE.

The sweet violet, *Viola odorata*, which is normally grown in large concrete tubs in the Gold Coast occasionally harbours infestations of the root-knot nematode. Some of the affected roots may exhibit typical galls while others on the same plant may become generally thickened in parts as already described in the case of onions, *Allium cepa*, when attacked by this parasite.

SUMMARY.

An account is given of observations on the occurrence of nematodes of the genus *Meloidogyne* in the Gold Coast. It includes a list of seventy-six host plants, both cultivated and wild, suitable for the sustenance and multiplication of the parasites as well as comments on the reactions of these various plant species to invasions of their root tissues. Many of the host plants listed constitute new records and the data submitted point to the conclusion that the root-knot eelworm has been long established in the Gold Coast.

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The “ Spring Rise ” in the Nematode Egg-Count of Sheep

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It has been shown that the number of helminth eggs passed in the faeces of Scottish hill sheep reaches a peak in May or early June (Morgan and Sloan, 1947; Cushnie and White, 1948; Morgan, Parnell and Rayski, 1950). More recently similar observations have been made on Halfbred sheep in South East Scotland (Parnell, Dunn and Mackintosh, 1954). Three main causes have been suggested for this marked rise in egg output: (a) an increase in the egg laying activity of worms already present (Taylor, 1935; Naerland, 1949; Cushnie and White, 1948); (b) an increase in the number of worms producing eggs, due to previously dormant larvae reaching maturity (Taylor, 1953); and (c) an increase in the total worm population due to reinfection at the time (Morgan, Parnell and Rayski, 1951). As the last authors have pointed out, the problem has an important bearing on the understanding of host-parasite relationships under grazing conditions and on the practical question of prophylactic anthelmintic treatment.

Recent work at the Grassland Research Station, Stratford-on-Avon, on grazing management as a control of worm-infestation, provided unusual opportunities for a study of the spring rise in egg output. This was chiefly because it was possible to study ewes, both in the field and in indoor pens, which were nevertheless not exposed to reinfection (Spedding, 1954a).

METHODS.

A number of groups of animals, employed in existing experiments, were selected for detailed observation during the late winter of 1953 and the spring of 1954. These groups differed in age of animal, type of management and diet, as described below.

Group 1. Five 3 year old Clun Forest ewes were folded over a worm-free field from 26th August, 1953, to 8th January, 1954. They were moved every two or three days, never returning to an area once grazed. This management appeared to prevent reinfection in a group of lambs grazing on the same field, (Spedding 1954a) and it is therefore probable that the ewes were free from reinfection over this period. They were dosed with phenothiazine on 31st October, 1953, and on 8th January, 1954, they were moved to indoor pens and fed on hay and silage. They remained on this diet until they lambed, in the middle of March, 1954, when crushed oats and cold-stored grass were added to the ration. During this time the pens were cleaned out every two days and the lambs raised worm-free, except for *Strongyloides papillosus* and an occasional *Trichuris ovis*. Regular egg-counts were carried out on the faeces of these ewes over the whole period studied (16th July, 1953 to 23rd June, 1954). A zinc sulphate flotation/centrifuge technique was employed, the eggs isolated from 1 gm. of faeces being counted. The trends in the average egg-output of the group, based on 145 individual counts, were therefore more reliable than the actual numbers found.

Group 2. Five Clun Forest ewes (3 yr. olds) were transferred to indoor pens as they lambed, in March, 1954. They had previously been grazed with the farm flock, which, partly due to dosing with phenothiazine in January and February, had a very low egg-count. They were fed on crushed oats, hay, silage and cold-stored grass. The pens were cleaned out as for Group 1 and the lambs raised worm-free to the age of 2 months, when they were experimentally infected. Egg-counts for the ewes were recorded from January to the end of June, 1954.

Group 3. Nine ewes (Clun Forest, 3 yr. olds) were moved to a worm-free field as they lambed, March, 1954, and folded across it, moving every two days. The late growth of grass at this time necessitated supplementary feeding of hay and silage, in addition to the usual crushed oats, for the first six weeks. The lambs grazing with these ewes remained worm-free (Spedding, 1954 b). Egg-counts were recorded from January to the end of June, 1954.

Group 4. Six Clun Forest ewe tugs were transferred to indoor pens on 22nd January, 1954. They were fed on hay and silage until 21st May; from this time they received a daily feed of fresh grass cut from a worm-free sward. Egg-counts were carried out from December, 1953 to the end of June, 1954.

RESULTS.

Group 1. The average egg-counts for this group are shown in Graph 1, in which times of dosing and lambing are indicated. The egg-counts were at all times low and 10 gm. samples of faeces were taken to allow of greater accuracy.

A minor peak occurred in the autumn of 1953, followed by a very low level until February. Although the latter coincided with a period of anthelmintic dosing, it will be noted that a period of six weeks elapsed between these doses, during which time the egg-count did not exhibit any marked rise. A distinct double peak occurred in the spring of 1954.

Group 2. The average egg-counts are shown in Graph 2. The two doses of phenothiazine were given the day after the first two low counts and were not, therefore, directly responsible for them.

A marked rise occurred in the spring of 1954, reaching a somewhat lower level again in June.

Group 3. These ewes also showed a marked spring rise in egg output (Graph 3) which declined in June.

Since their lambs were raised worm-free, it may be assumed that these animals received no reinfection from the middle of March, 1954, onwards.

Group 4. The average egg-counts for these animals (Graph 4) exhibited a spring rise at about the same time as Groups 1, 2 and 3. It was, however, of brief duration.

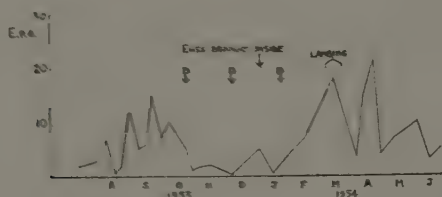
TABLE I.
Individual e.p.g. counts for Group 4.

| Sheep No. | Date | | | | | | | |
|--------------|----------|--------|------|-----|------|------|------|---------|
| | 11/12/53 | 4/1/54 | 16/1 | 3/2 | 24/2 | 31/3 | 12/4 | 23/4/54 |
| 28 | 0.4 | 3 | 0.8 | 0.8 | 4.2 | 2 | 23 | 16 |
| 41 | 0.5 | 0.4 | 1.7 | 0.8 | 1.6 | 25 | 15 | 13 |
| 20 | 0.2 | 0.4 | 31 | 2.2 | 0.6 | 69 | 50 | 11 |
| 69 | 0 | 0.8 | 0.2 | 0 | 0 | 27 | 88 | 1 |
| 18 | 4 | 0 | 0 | 1.2 | 1.8 | 8 | 374 | 43 |
| 19 | 0 | 0 | 0.2 | 0 | 0 | 0 | 7 | 17 |
| Group | | | | | | | | |
| Mean : | 0.9 | 0.8 | 5.6 | 0.8 | 1.4 | 22 | 93 | 17 |

Since the validity of this peak depends largely upon one average count, the complete data over this period are tabulated in Table I.

DISCUSSION.

The lambs in Group 1 were raised worm-free and it may be assumed, therefore, that the ewes were maintained under conditions precluding reinfection from the time they were brought in on 8th January, 1954. In view of their previous management, it is unlikely that they acquired any infective larvae from 26th August, 1953. The spring rise in their egg output cannot, therefore, have been due to an increase in the worm-population at the time. It appears unlikely that the rise was due to dormant larvae acquired in the previous August. The most probable explanation is an increase in the egg output of the existing worm-burden. The initial peak in late March coincided with lambing and it is possible that this imposed a strain on the animals, tending to a reduction of their powers of resistance. Similarly, in Groups 2 and 3,

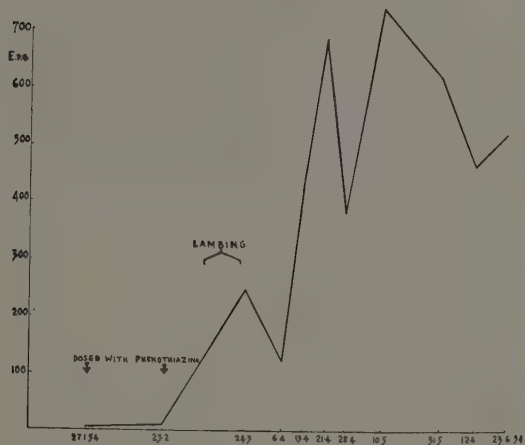


Graph 1.—Average egg-count of group 1.

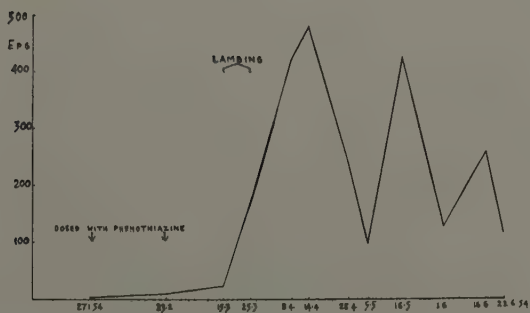
D = dosed with phenothiazine.

the first indication of a spring rise was coincident with lambing. This is in agreement with the observation of Parnell, Dunn and Mackintosh (1954) that the onset of the spring rise was closely correlated with the date of parturition. In Group 4, however, no lambing occurred.

In Group 2, the rise was coincident also with a change in diet, from fresh grass to hay and silage. This reduction in the feeding value of the diet at lambing time would be expected to produce an increase in egg output (White and Cushnie, 1952). In Group 1, however, the diet was improved at this time by the addition of crushed oats and cold-stored grass, while in Group 4, the diet remained constant during this period. The last Group (4), therefore, exhibited a small rise although no lambing strain occurred and their diet remained unchanged from 22nd January to 21st May.

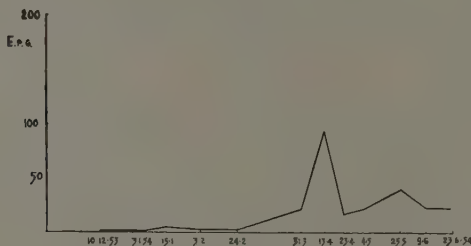


Graph 2.—Average egg-count of group 2.



Graph 3.—Average egg-count of group 3.

It is not impossible that larvae acquired towards the end of the previous year might have remained in an inhibited state until April. However, maintained indoors with reinfection improbable from the end of January, the most likely explanation is, again, an increase in egg-production by the existing worm-population. Groups 1, 2 and 4 received no fresh grass during the spring and are, therefore, not strictly comparable with sheep in the field. Group 3, by contrast, never left the field and had access to fresh grass before and after lambing. The marked spring rise in their egg output, therefore, occurred under grazing conditions but without any reinfection at the time. This, and the rise

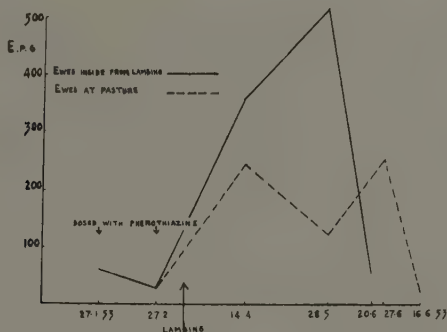


Graph 4.—Average egg-count of group 4.

in egg output of Group 2, could have been due to dormant larvae reaching maturity and thus adding to the egg-laying worm population. Considering all four groups, however, it appears certain that a spring rise can occur where no infective larvae are acquired since the previous autumn. Such a rise, therefore, may be caused by an increase in the egg-production of the existing worm-population. In the spring of 1953 it was noted that a spring peak occurred in May both in field sheep and in those maintained indoors on hay, silage and cold-stored grass. The increase was greater in the indoor animals (Graph 5). This indication that a less nutritious diet causes an increase in the magnitude of the spring rise is supported by the fact that the egg-counts of Group 2 reached a much higher level than those of Group 3.

It is possible that, in the field, an increase in worm-population, by direct reinfection and by the addition of previously dormant larvae, and an increase in the rate of egg-production by the existing worm-

population, all play their part in producing the spring rise. This, in turn, may be exaggerated by the stress of lambing and any lowering of the nutritional level.



Graph 5.—Average egg-count of indoor and outdoor groups of ewes.

Although it appears certain that an increase in the rate of egg output by the worm-population can occur in the spring, it does not necessarily follow that it does occur where the population is being increased by normal reinfection.

SUMMARY.

1. Observations carried out on four groups of sheep during the spring of 1954 are described.

2. A spring-rise in the worm-egg output was found to occur in all the groups studied.

3. The management of the animals precluded reinfection during the spring and, in two instances, from 8th January and 22nd, respectively.

4. Time of lambing and nutritional level appeared to influence the onset and magnitude of the spring increase.

5. It appeared certain that the absence of reinfection at the time did not prevent a spring rise and it appeared probable that, in the sheep studied, the rise was due to an increase in the egg output of the existing worm-population.

ACKNOWLEDGMENTS.

The authors wish to thank the Director, Dr. William Davies, for facilities granted, and Mr. G. Pearson Hughes for his advice and encouragement.

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The Control of Worm-infestation in Sheep by Grazing Management

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Previous studies on the effect of a sub-clinical worm-burden on the productivity of sheep (Spedding 1952a, 1953) have suffered from two major disadvantages. Either they have depended upon indoor experiments, using a worm-free control group, or they have relied upon faecal egg-counts to distinguish two levels of infestation. As pointed out by Whitlock (1949), the results of the former method are not necessarily applicable to pasture-fed animals. The latter method is uncertain because of the difficulty of distinguishing true differences in faecal egg-counts at a sub-clinical level (Spedding, 1952b). The experiment here described was designed to overcome these disadvantages.

METHODS.

Ten pairs of twin lambs, Clun Forest, with the exception of one pair of Suffolk x Halfbred, were raised worm-free in indoor pens up to the age of two months. At this time a small quantity of infected grass was fed, which resulted in an average egg-count of 15 eggs per gram (e.p.g.) at weaning time, when the animals were four months old. Immediately after weaning the lambs were separated into two groups (A and B), one member of each twin pair being allocated to each group and balanced as closely as possible for sex, average weight and distribution of weight within the group. To establish a difference in the levels of infestation Group B lambs were grazed for $3\frac{1}{2}$ days (August 1–4, 1953) on a pasture previously grazed by sheep. This was intended to allow the establishment, by normal grazing, of a very low level of infestation. On 4th August both groups were moved on to a newly sown ley, dominantly white clover, that had not previously held stock of any kind. The two groups were pastured in adjacent paddocks using a hurdling system consisting of movable wire netting fences and iron posts. The groups were moved simultaneously every two days to a fresh area, never returning to the pasture once this had been grazed: the purpose of this management being to prevent, if possible, any reinfection taking place.

As a comparison between these conditions and those involving constant reinfection, two further groups (C and D) of lambs were grazed two paddocks behind Groups A and B. Group C grazed two paddocks behind Group A and was, therefore, exposed to a negligible infection. Group D was grazed two paddocks behind Group B and was exposed to whatever infection resulted from the higher egg-output of Group B. A plan of the grazing management is shown in Fig. 1.

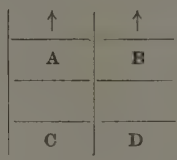


Fig. 1. Relative positions of Groups A, B, C and D during grazing.

Groups C and D consisted of six twin lambs each, allotted as in Groups A and B. They were, however, raised in the field and carried a light worm infestation.

This method of management was continued for four months, from 4th August until 8th December, 1953. The paddocks were of such a size that ample grazing was available at all times for the two following groups. Individual weights and egg-counts were recorded throughout the experimental period.

Results: Groups A and B.

The average liveweight curves for Groups A and B are shown in Graph 1 and the average liveweight gain for each animal is given in Table I.

The effect of the infection acquired by Group B was clearly reflected four weeks later in the lower rate of liveweight gain. The difference, though consistent, was never great and, at the end of the experiment, Group A had gained an average of 5.5 pounds per head more than Group B. This difference was significant at the 5 per cent. level. The average egg-counts for these two groups are shown graphically (Graph 2); they represent the total e.p.g. counts with the exception of *Strongyloides papillosus*, which did not appear conspicuous in either group.

The average egg-counts of Group A were remarkably constant and extremely low, indicating fairly positively that no reinfection had occurred. Those of Group B rose rapidly to a peak and steadily fell during the course of the experiment to a low level. A marked difference in faecal consistency between the groups was observed. The majority of the lambs in Group B scoured frequently, while no animal in Group A suffered in this way.

TABLE I.
Liveweight Gain of Groups A and B (in pounds)
* Suffolk X Halfbred
†W = Wether; E = Ewe

| Group | Lamb No. | Sex | Liveweight gain in pounds | Group Mean | S.E. | Difference between | |
|-------|----------|-----|---------------------------------|---------------|--------|--------------------|--------|
| | | | | | | Twins | Groups |
| A | 4* | W† | 59.1 | 44.0 | ± 1.60 | + 12.2 | + 5.5 |
| | 7 | E | 37.5 | | | + 11.0 | |
| | 8 | W | 47.0 | | | + 5.7 | |
| | 11 | E | 35.8 | | | — 7.7 | |
| | 13 | E | 48.0 | | | + 13.1 | |
| | 15 | E | 43.2 | | | — 1.3 | |
| | 26 | W | 41.6 | | | + 7.1 | |
| | 29 | W | 36.5 | | | + 3.2 | |
| | 32 | E | 44.7 | | | — 1.4 | |
| | 34 | E | 46.3 | | | + 12.7 | |
| B | 5* | E | 46.9 | 38.5 | ± 1.60 | + 5.5 | + 5.5 |
| | 6 | E | 26.5 | | | | |
| | 9 | W | 41.3 | | | | |
| | 10 | W | 43.5 | | | | |
| | 12 | W | 34.9 | | | | |
| | 14 | W | 44.5 | | | | |
| | 27 | E | 34.5 | | | | |
| | 30 | E | 33.3 | | | | |
| | 31 | W | 46.1 | | | | |
| | 33 | E | 33.6 | | | | |

Groups C and D.

From Table II it will be seen that the difference in liveweight gain was greater between Groups C and D, but the variability within each group was markedly higher. This difference was not significant and

the slightly higher level of the egg-counts in Group D (Table III) did not suggest a difference in worm-burden likely to produce such a depression of liveweight gain.

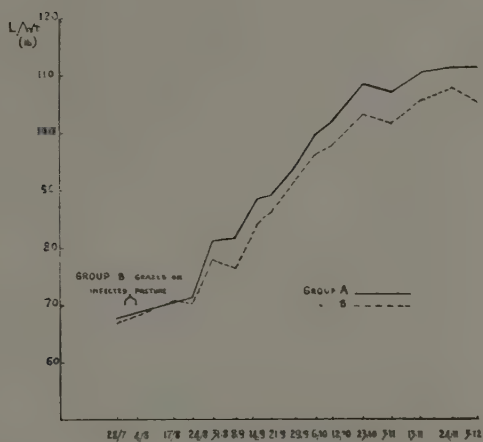
TABLE II.
Liveweight Gain of Groups C and D (in pounds)
* E = Ewe; W = Wether

| Group | Lamb No. | Sex | Liveweight gain in pounds | Group Mean | S.E. | Difference between | |
|-------|----------|-----|---------------------------------|---------------|--------|--------------------|--------|
| | | | | | | Twins | Groups |
| C | 25 | E* | 27.4 | 21.0 | ± 4.46 | + 9.9 | + 9.5 |
| | 43 | W | 20.0 | | | — 0.7 | |
| | 50 | E | 10.9 | | | + 7.7 | |
| | 53 | W | 21.8 | | | + 5.4 | |
| | 57 | W | 39.7 | | | + 39.0 | |
| | 63 | E | 6.0 | | | — 4.6 | |
| D | 24 | E | 17.5 | 11.5 | ± 4.46 | | + 9.5 |
| | 42 | W | 20.7 | | | | |
| | 49 | W | 3.2 | | | | |
| | 54 | E | 16.4 | | | | |
| | 58 | E | 0.7 | | | | |
| | 64 | W | 10.6 | | | | |

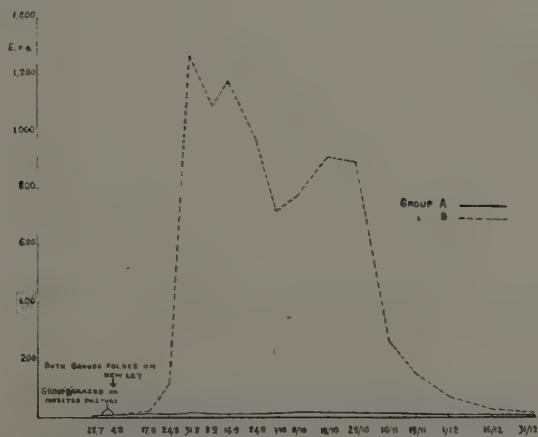
TABLE III.
Average e.p.g. counts for Groups C and D.

| Group | Date | | | | | | | | | | | | | | | |
|-------|---------|-------|-------|-------|------|-------|-------|-------|-------|--------|--------|--------|--------|--------|-------|--------|
| | 5/8/53. | 20/8. | 24/8. | 31/8. | 8/9. | 14/9. | 21/9. | 1/10. | 8/10. | 13/10. | 19/10. | 29/10. | 10/11. | 19/11. | 5/12. | 16/12. |
| C. | 30 | 3 | 10 | 44 | 31 | 38 | 81 | 36 | 32 | 33 | 34 | 37 | 37 | 11 | 10 | 1 |
| D. | 28 | 4 | 29 | 54 | 72 | 36 | 76 | 50 | 75 | 55 | 86 | 66 | 18 | 28 | 30 | 5 |

Following this first experimental period, Groups A and B were maintained on separate paddocks on a previously ungrazed pasture from the middle of December, 1953, until June, 1954. Each group, therefore, was exposed to a rate of reinfection dependent largely on its average egg-count when first placed on the paddocks. This period was chiefly of interest from a management point of view. At the end of this time Group A weighed, on the average, 8.6 lb. per head more than Group B, and when sheared, the average fleece weight for Group A was 0.9 lb. per head heavier than that of Group B. These differences, however, cannot be attributed with any certainty to either a persistence of the



Graph 1.—Average L/Wt. gain of groups A and B.



Graph 2.—Average egg-counts of groups A and B (1953).

effects of the first period or to a subsequent effect during the second period.

The subsequent egg-counts (Graph 3) are of interest on account of their completely separate curves. The latter indicated that even a small difference in egg-count in December had a measurable influence on the subsequent level of infestation under these conditions of set-stocking.

No animal, in either group, was dosed with anthelmintics at any time.

DISCUSSION.

The depression of liveweight gain in Group B was of interest since it occurred as a direct result of the $3\frac{1}{2}$ days' infection from pasture previously grazed by sheep and took place regardless of the high quality of the pasture subsequently grazed. The egg-count data for Groups C and D suggest that these animals followed Groups A and B too closely to be exposed to the large difference in infection that the faeces of Groups A and B might have been expected to produce. The low level of egg output in Group A indicated that (*a*) the pasture used was probably worm-free and (*b*) the method of management prevented reinfection. This was supported by the fact that several animals in Group A passed faeces with negative counts towards the end of the experiment.

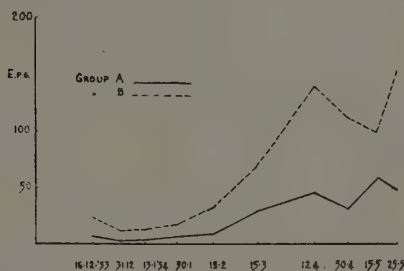
It was concluded that, even at low levels of infestation in the field, the infected lambs gained weight at less than their optimum rate, that the management used was capable of preventing reinfection, and that the pasture was, in the first instance, worm-free. This last factor is important as the ley used was a direct reseed following a wheat crop which was grazed in the stubble by sheep in September, 1952. It was, therefore, first grazed only 11 months after the land had last carried sheep.

The possibility of applying this type of management on a worm-free field to ewes and lambs, in an endeavour to prevent infection of the lambs, is at present being investigated.

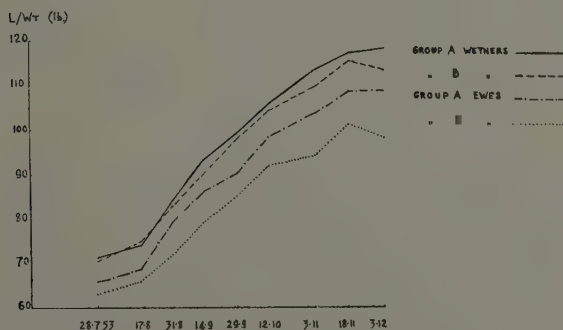
The experiment described provided information on two further points. First, the management appeared to make possible a study of the course of an infestation in animals grazing at pasture, without the complication of reinfection by the same or other species of parasitic nematodes. Thus the egg-count curve of Group B (Graph 2) represented the development of their mixed infestation, in terms of egg

output. The low level finally reached, however, would seem capable of persisting for some time, as shown by the curve for Group A.

Secondly, there appeared to be a differential effect of worm-infestation on wethers and ewes. Table I shows that in most cases the



Graph 3.—Average egg-counts of groups A and B (1954).



Graph 4.—Liveweight gain of ewe and wether lambs in groups A and B.

control lamb gained more weight than its twin. In every pair of twins in Groups A and B the control gained more than its twin where the twins were of the same sex or where the control was a wether and its twin a ewe. Where the more infected animal gained slightly more than its control, the former was a wether and the latter a ewe. This was

probably due to the greater rate of liveweight gain of wethers at this age. In Group A, however, the wethers gained an average of 3.5 lb. per head more than the ewes, while in Group B the wethers gained an average of 7.1 lb. per head more than the ewes. Thus, comparing the wethers, those of Group B suffered an average depression of liveweight gain of 4.0 lb. per head; while in the ewes, those of Group B gained an average of 7.6 lb. per head less than those of Group A (Graph 4). This may suggest that the ewes were adversely affected by the worm-infestation to a greater degree than the wethers, and this suggestion is supported by the consistent trends observed in the direction of these differences. The difference between twins, however, was inseparable from that between sexes and, statistically, there was no real evidence to support the suggestion.

SUMMARY.

1. A method of management of sheep at pasture is described which appeared successful in preventing reinfection by nematodes parasitic in the alimentary tract, with the exception of *Strongyloides papillosus*.

2. A significant depression of liveweight gain was observed, due to a sub-clinical infestation in lambs at pasture.

3. Reseeded pasture sown on land that had carried sheep 11 months before appeared to be worm-free.

ACKNOWLEDGMENTS.

The author's thanks are due to the Director, Dr. William Davies for facilities granted; to Mr. G. Pearson Hughes for his helpful advice; to Mr. T. H. Brown for his assistance throughout this work; and to Mr. C. D. Kemp for the statistical treatment of the results.

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Stem Eelworm Attacking Carrots

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In July, 1952, carrots growing in the Chatteris area of the Isle of Ely were found to be attacked by *Ditylenchus dipsaci*. The preceding crop had been wheat and for the previous twenty years the crop rotation of the field had been carrots, potatoes and wheat with an occasional crop of celery. There have been two previous records of stem eelworm attack on carrots in this country, both from the Chatteris area, the first in 1931 and the second in 1941. These occurred on fields which, both before and since the attacks, have grown carrots frequently. The outbreak was very severe in 1941 and caused slight damage in later years but appears since to have died out. All three outbreaks were on different fields on different farms although within the radius of about one mile. The fields are separated either by a railway line or a wide ditch as well as a series of minor ditches, and it is difficult to see any connection between the outbreaks.

The leaf bases were swollen and puffy and the infestation often extended downwards into the top of the root. Both the leaf bases and the crown were paler than normal and, as the attack progressed, they became brown and decayed. The attack was not noticed by the farmer until the crop was being harvested when the tops of affected carrots broke off leaving the roots in the ground. For this reason the extent of the damage could not be clearly seen but it appeared that the attack was most severe in the lowest part of the field. These symptoms were essentially the same as those described and figured by T. Goodey (1931).

Attacked carrots were replanted at Rothamsted and in the following year several produced flowering stems. Many of these were deformed and twisted with some stunting and swelling. In some plants the stem and bracts just beneath the umbel were swollen and had brownish lesions. Later the seed from these heads was collected and dried. In

the spring of 1954 this seed was sown but although 89 seeds were planted not a single infested carrot resulted. Seedborne infestation therefore remains unproven.

Infested carrots were chopped up and used to inoculate pots of J. I. compost in which were grown carrots, potatoes, celery, parsley, parsnips and garden peas. The carrots in the inoculated pots died after a few weeks whereas those in the uninfested control pot grew normally. Four potatoes were planted, one being a control which grew to a height of 14 inches, whilst the plants in the inoculated pots were severely damaged and averaged $3\frac{1}{2}$ inches high. The leaflets were malformed and twisted and there were puffy and cracked brownish areas on the backs of the leaves. Stems and petioles had gall-like swellings which developed into lesions. Some shoots had the terminal bud destroyed so that they yellowed and died prematurely. In others, the death of the terminal bud caused laterals to develop. When the pots were turned out, all the new tubers were clean, except one, in which a small lesion contained a few adults, larvae and eggs of *D. dipsaci*. A slight attack developed on the celery as somewhat misshapen and crinkly leaflets and there were swellings on the petioles. In one plant considerable dwarfing occurred as a result of the infestation. Neither parsley nor parsnips were attacked but garden peas were dwarfed and swollen with numerous eelworms in the tissue.

The farmer kindly allowed us in April, 1953, to put down an experiment on the field, which in that year was growing potatoes. Four replicated blocks of plots, each of four rows, 12 ft. long, of the following 12 plants were sown: Parsnips, celery, parsley, kidney beans, garden peas, field beans (*Vicia faba*), broad red clover, late-flowering red clover, lucerne (variety Du Puits), oats (variety S. 147), sugar beet and mangolds. A row of carrots was sown between each plot and along each edge. The plants were examined from time to time and, as late as the beginning of August, apart from a few celery plants which had lesions containing eelworms at the leaf bases, all the other plants appeared healthy and were growing excellently. The field beans were over 4 ft. high and, although apparently healthy, one plant was found with a long blister-like lesion on the stem about 18 ins. above the ground. Examination showed the lesion to be full of stem eelworm. Another examination in early September brought to light many more lesions on bean stems and a few more celery plants were found attacked including one or two with small, isolated, petiolar lesions. On this occasion many carrots were dug and some of these were found to be typically attacked.

The other test plants and the potatoes adjoining the experiment were apparently quite free from eelworm attack.

The presence of blister-like lesions on the bean stems suggested that the race of *D. dipsaci* might be the giant one (Goodey 1941). In 1954 a pot experiment was set up to test this supposition and also to make certain that the eelworms attacking carrots and beans in the field at Chatteris were identical. For ease of reference the population from this field will be called "race 'X'." Pots of carrots and broad beans (*V. faba*) were inoculated with about 10,000 eelworms each, extracted from beans infested with race 'X' and compared with a similar series inoculated with the same numbers of the giant race extracted from infested bean material obtained from Portugal. In addition, some pots of oats (var. Golden Rain) were inoculated with race 'X.' The results were as follows :

RACE 'X.'

Carrots.

Malformation and lesions on the leaf bases. Ultimately the eelworms invaded the tops of some of the roots.

Broad Beans (*V. faba*).

Blister-like lesions on the lower parts of the stems and broken black lesions at the stem bases.

Oats.

Typical symptoms of tulip root.

GIANT RACE.

Carrots.

These remained clean throughout the experiment.

Broad Beans (*V. faba*).

Blister-like lesions on the lower parts of the stems though one lesion was 15 ins. above the ground. One plant was very dwarfed and malformed. A few had broken black lesions at the stem bases.

Infested material from this experiment was teased out in water and samples of adult eelworms picked up, relaxed by gentle heat and then fixed in 5 per cent. formalin. Measurements were obtained from camera lucida drawings and these are set out in Table I.

DISCUSSION.

Certain conclusions can be drawn about the population of stem eelworm (Race 'X') which was found attacking carrots near Chatteris. The evidence from the measurement data and the fact that the giant race did not attack carrots indicates that race 'X' is not identical with the giant race. The fact that eelworms from infested bean material obtained from the carrot field transferred to carrots confirms that race 'X' is not a mixed population. The damage to the stem bases of *Vicia faba* was typical of the oat race but the production of blister-like lesions generally higher up the stem was not characteristic. Large numbers of eelworms were to be found immediately below the epidermis in the region of these lesions. White cottony masses of eelworms were easily visible in this position when the epidermis was peeled off. The giant race also behaves in this way. Typical tulip-root symptoms were produced on oats grown in pots whereas those on the field site showed no signs of attack. The two oat varieties used, S.147 on the field site and Golden Rain in pots are both very susceptible to the oat race. The eelworms from these pot-infested oats were slightly longer than race 'X' from carrots and beans and since they were reproducing quite well it is obvious that oats were a favourable host under these conditions. Table II sets out a comparison of the body lengths of samples of the giant race from *V. faba* and race 'X' from *V. faba* and oats, with similar data from T. Goodey (1941). The close agreement between the two series is remarkable.

Under pot conditions carrots, celery, *V. faba*, garden peas, oats and potatoes were attacked. In the field, however, only carrots, celery, *V. faba* and one specimen of fools parsley (*Aethusa cynapium*) were found attacked, although the same series of plants was grown as well as a number of others.

The inconsistencies between the two sets of results need to be explained. In pots, carrot seedlings were wiped out in the 1952 experiments so that, compared with the field experiment where only a small percentage of the carrots was attacked, it seems reasonable to assume that the level of infestation was much higher in the pots. The same line of argument may be applied to the question of the oats, garden peas and potatoes but it is not clear why these crops remained apparently completely free from eelworm attack in the field. Celery and *V. faba* were attacked both in pots and in the field.

Potatoes are not a recognised host of the oat race and attack on celery has not been reported before in this country. Peas have been reported as attacked by stem eelworm on several occasions and in 1952 one of us (J. B. G.) successfully transferred an infestation from peas to oats, setting up typical tulip-root. Although *V. faba* and parsnip are

TABLE I.

Summary of data on carrot population of *D. dipsaci* (Race "X") compared with data on giant race.

| Race | Source | Host | Sex | L. | Standard deviation | | | a. | b. | c. | V% |
|-------|-----------|----------------|-----|------|--------------------|----|------|------|------|------|----|
| | | | | | n. | | | | | | |
| " X " | Chatteris | Carrot | ♀ | 1.37 | 0.258 | 12 | 44.0 | 7.35 | — | 80.5 | |
| " X " | Chatteris | Oats | ♀ | 1.52 | 0.090 | 12 | 43.8 | 7.22 | — | 80.7 | |
| " X " | Chatteris | <i>V. faba</i> | ♀ | 1.36 | 0.098 | 12 | 36.3 | 6.83 | — | 81.0 | |
| Giant | Portugal | <i>V. faba</i> | ♀ | 1.86 | 0.129 | 7 | 53.4 | 7.74 | — | 81.4 | |
| " X " | Chatteris | Carrot | ♂ | 1.27 | 0.024 | 12 | 45.3 | 6.75 | 14.4 | | |
| " X " | Chatteris | Oats | ♂ | 1.49 | 0.024 | 12 | 50.4 | 6.78 | 15.6 | | |
| " X " | Chatteris | <i>V. faba</i> | ♂ | 1.33 | 0.167 | 12 | 41.2 | 6.44 | 14.2 | | |
| Giant | Portugal | <i>V. faba</i> | ♂ | 1.63 | 0.021 | 3 | 50.0 | 7.21 | 18.4 | | |

NOTE.—L = length in mm.; a = length/greatest width; b = length/length of oesophagus; c = length/tail length; V% = position of vulva as % of length.

TABLE II.

Comparison of mean lengths (mm.) of *D. dipsaci* obtained in this work, with those from T. Goodey (1941).

| Origin of data | Race | Host | Female | | | Male | | |
|----------------|-------|----------------|--------|------------|----|------|------------|----|
| | | | L. | Stan. dev. | n. | L. | Stan. dev. | n. |
| This work | "X" | Oat | 1.52 | 0.090 | 12 | 1.49 | 0.024 | 12 |
| T.G. | Oat | Oat | 1.49 | 0.076 | 50 | 1.38 | 0.087 | 50 |
| This work | "X" | <i>V. faba</i> | 1.36 | 0.098 | 12 | 1.33 | 0.167 | 12 |
| T.G. | Oat | <i>V. faba</i> | 1.38 | 0.141 | 82 | 1.33 | 0.096 | 85 |
| This work | Giant | <i>V. faba</i> | 1.86 | 0.129 | 7 | 1.63 | 0.021 | 3 |
| T.G. | Giant | <i>V. faba</i> | 1.97 | 0.156 | 35 | 1.73 | 0.151 | 37 |

recognised hosts of the oat race, symptoms on *V. faba* were not entirely characteristic and parsnips remained unattacked both in pots and in the field. It seems probable, therefore, that although it would attack oats and beans, the race 'X' population was not covered by the term 'oat race' of stem eelworm,

Carrots were grown on the field again in 1955 and were severely damaged in the same areas as previously. As a check a few short rows of oats (Sun II) were sown in one of the affected areas. These oats grew normally in the first few weeks but tulip-root symptoms appeared on a very small percentage of the later tillers. The eelworms were breeding in these tillers and numerous eggs were present. This slight and late development of tulip-root in the oats, taken together with the previous observations on oats inoculated with this population of stem eelworm, adds further weight to the suggestion that the 'X' race of *D. dipsaci* is not one covered by the term 'oat race' of stem eelworm.

ACKNOWLEDGMENTS.

Thanks are due to Mr. H. J. Eaton of the N.A.A.S. for bringing this attack to our notice and especially to Mr. A. S. Rickwood for his willing co-operation in arranging the field experiment on his infested field.

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A Routine Method for the Maintenance of *Schistosoma mansoni* *in vitro*

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A review of the methods by which schistosomes have been maintained *in vitro* and the present method evolved, has already been published (Newsome and Robinson, 1954). It was felt advisable to employ a natural medium, serum, for the culture of *Schistosoma mansoni* *in vitro*, and to study in this medium as many aspects as possible of the physiology of the worms, before trying to use a synthetic medium. The information gained by such a study would be expected to assist in working out the composition of a suitable synthetic medium.

The present paper gives a detailed account of the methods used for setting up the culture apparatus, and for removing the worms from the host. As a preliminary to a comparative study of carbo-hydrate metabolism in cultured and uncultured worms, their glycogen content has been investigated.

METHOD OF ASSEMBLY AND STERILIZATION OF APPARATUS.

The apparatus is shown in Fig. 1. Its principal parts and their uses have already been described (Newsome and Robinson, 1954). In view of the difficulties which have been experienced in obtaining a sterile culture, it is necessary to sterilize all parts of the apparatus before finally assembling and autoclaving, if sterility is to be assured. The following components are therefore sterilized by dry heat at 160°C for 1 hour.

- a. The apparatus without caps or stoppers, apertures being plugged with cotton wool.
- b. Two air inlets.
- c. A 100 ml, conical flask.
- d. Two fine hypodermic needles.

The following components are sterilized by autoclaving.

a. A 14 cm. Seitz filter with a divided outlet ; one arm of this bears the vaccine cap fitting the neck of the reservoir, the other a rubber bung to fit the 100 ml. conical flask. **b.** The ground glass cap of the introduction chamber complete with pipette bulb. **c.** A vaccine cap to fit the withdrawal arm. **d.** The rubber " policeman."

The operations which follow are then carried out in the bacteriological cabinet which is first irradiated for 15 minutes by a mercury vapour lamp stated by the makers to give 100 microwatts / cm² at 1 metre on 2537 Å°.

1. The large vaccine cap on one arm of the Seitz filter is fitted into the neck of the reservoir.
2. The rubber stopper on the other arm is inserted in the neck of the 100 ml. flask.
3. An air inlet is inserted through the stopper of the flask.
4. The stopper of the introduction chamber is placed in position, but, between its inner surface and the outer ground glass surface of the top of the withdrawal chamber, is placed the shaft of a hypodermic needle, held in place by a strip of cellulose tape.
5. The small rubber cap on the withdrawal arm is placed in position and a hypodermic needle placed between the rubber and the glass. The cap and the needle are held lightly in place by cellulose tape.

The assembled apparatus is placed in the autoclave together with a Petri dish of petroleum jelly and a small brush. Steam is allowed to issue freely for a period of 20 minutes before sterilization begins at a pressure of 15 lbs. and temperature of 250°F for 20 minutes. After sterilization, the autoclave is opened as soon as the pressure reaches zero, and the following operations quickly carried out in the autoclave.

1. The exposed region of the ground glass outer surface of the introduction chamber is coated thinly with petroleum jelly, the hypodermic needle removed, and the glass cap fitted firmly in place.
2. The hypodermic needle is removed from the withdrawal arm and the cap fitted firmly in position.

On the bench, the cap of the reservoir is wiped with an alcohol swab, an air inlet inserted, and the arm leading to the reservoir clamped

off, so that the first medium to be filtered (containing any impurities from the Seitz pad), will enter the 100 ml. flask. Filtration then proceeds under a positive pressure of between 100 and 150 mm. Hg. When approximately 40 ml. have been filtered, the arm leading to the side flask is clamped off and the other arm simultaneously opened. When the reservoir is about half full, the cap on the withdrawal arm is wiped with an alcohol swab and a hypodermic needle attached to a 10 ml. syringe inserted; as air is withdrawn from the main stem of the apparatus, the worm chamber and withdrawal arm fill with medium. Pressure is applied to the pipette bulb on the cap of the introduction chamber and air is forced into the reservoir; on relaxing the pressure, the chamber fills with medium to the required level. Filtration continues until the level of medium reaches the base of the neck of the reservoir. The arm leading from the Seitz filter is then clamped off with a screw clip and the tubing cut above the clip.

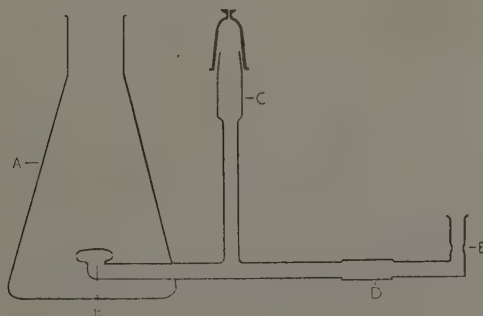


Fig. 1.—The Apparatus.

A. The reservoir. B. The glass "filter." C. The worm introduction chamber. D. The worm observation chamber. E. The withdrawal arm.

The apparatus together with the sterile "policeman" is placed in the bacteriological cabinet; it is masked from the rays of the mercury vapour lamp and the cabinet is irradiated for 15 minutes. The rubber tubing leading to the reservoir is removed and the "policeman" slipped over the glass tubing. The apparatus is then incubated at 37°C and on attaining this temperature is ready for the insertion of the worms.

METHOD OF REMOVAL OF LIVE *S. mansoni* FROM THE HOST.

Golden hamsters (*Mesocricetus auratus*) were infected percutaneously with 150 cercariae of an Egyptian strain of *S. mansoni*, and sacrificed 8–12 weeks after infection. Perfusion techniques such as those of Yolles, Degiusti, Meleney and Ripsom (1947), although effective in recovering all the worms, were unsuitable, because of the time required for their successful operation. For culture work a yield of a few pairs of worms is sufficient, the important factor being their rapid and safe arrival in sterile fluid.

Both citrate/saline and citrate/Tyrode solution have been used as fluids in which to receive the worms on their emergence from the portal vein. Although no ill effects on the worms could be detected after a brief period in these fluids their use was discontinued and heparin/Tyrode substituted in view of the observation of Yolles *et al* (1947) that sodium citrate interferes with the oxygen uptake and glycolysis of *S. mansoni*.

Method.

1. The hamster is killed by ether, immersed in alcohol and pinned to a dissecting board.
2. The skin over the thorax and abdomen is quickly removed, the animal cauterized down the mid line, and transferred to the bacteriological cabinet.
3. The preparation is masked from the rays of the mercury vapour lamp, the air atomized and the cabinet irradiated for 15 minutes.
4. The operator having scrubbed up, sterile towels are laid, the thoracic and abdominal cavities opened along the mid line, and the ventral wall of the thorax removed.
5. The posterior vena cava is then clamped at two points with small artery forceps; one just anterior to the point of entry of the right renal vein, and one between the liver and heart.
7. The aorta is also clamped in the thorax region.
8. Heparin/Tyrode solution 1 : 50 is sprayed over the viscera in the region of the portal vein and the latter cut, care being taken to avoid damage to worms present in the vein.

9. Worms emerging from the cut ends of the vein are quickly transferred, on a mounted needle, to a Petri dish containing sterile Tyrode solution maintained at 37°C on a warm stage.

The apparatus is now inserted in the cabinet, the Petri dish containing the worms is masked, the cabinet irradiated as before, and the following operations carried out.

1. The glass cover of the introduction chamber is flamed to melt the petroleum jelly and facilitate its rapid removal.
2. Each pair of worms or single worm is removed from the Petri dish separately on a mounted needle, and inserted in the medium in the introduction chamber. The mouth of the chamber is flamed and the glass cap replaced after each insertion.

The apparatus is then removed from the cabinet and tilted so that the worms slip along the main stem and enter the observation chamber. The culture is maintained at 37°C in an incubator, and 3–5 ml. of medium are withdrawn daily through the withdrawal arm by means of a syringe and needle, to give the worms a change of medium.

RESULTS OBTAINED WITH DIFFERENT MEDIA.

1. *Horse serum/Tyrode solution 1 : 1.*

Although the worms survived in this medium for a few weeks on a number of occasions, the results on the whole were unsatisfactory, as the outcome was always uncertain. Change of pH after a few days incubation was often considerable, and although attempts were made to buffer the medium with phosphate buffers there was no increase in the efficiency of the medium.

2. *Undiluted normal horse serum.*

In this medium worms exhibited normal motor patterns and survived for periods of up to two months. It was decided to test the effect of adding substances normally present in the portal vein in greater concentrations than, or totally lacking in, the serum.

a. *Haemoglobin.*

On no occasion could any improvement in the efficiency of the medium be observed by the addition of small quantities of haemoglobin. Addition of haemoglobin in a concentration similar to that in the blood was impractical.

b. *Glucose.*

The effect of the addition of 0.1 per cent. glucose was immediately observable. On every occasion it was found that throughout the course of an experiment the activity of the worms was considerably greater than in horse serum without added glucose.

3. *Normal human serum.*

Without the addition of glucose, the results were similar to those obtained with horse serum, and addition of 0.1 per cent. glucose was beneficial. Addition of haemoglobin did not appear to increase the efficiency of the medium.

OBSERVATIONS ON CULTURED *S. mansoni*.

1. *Egg laying.*

In cultures maintained in both human and horse serum, eggs have been observed on numerous occasions. They have, macroscopically, the appearance of normal eggs of *S. mansoni*, but no attempt has yet been made to observe whether they are fully embryonated, or whether egg laying continues throughout the life of the worms *in vitro*. Location of eggs is assisted by mounting a cover glass in balsam on top of the worm chamber.

2. *Copulation.*

Copulation *in vitro* between adult male and female *S. mansoni* worms occurred fairly frequently in the culture apparatus, and the observations recorded were similar to those described by Chu (1938) for *S. japonicum*, except that the coupling extended for periods of up to eight days. When contact was made between male and female worms, the activity of the male was considerably increased. After taking a portion of the body of the female into the gynaecophoric canal, the male appeared, by contracting and expanding the canal, to draw in the body of the female.

3. *Effect of temperature.*

Increases of temperature even if small and of short duration usually resulted in the death of the worms. Decreases in temperature on the other hand even for long periods appeared to have no harmful effect. On one occasion worms were subjected to a temperature of approximately 20°C for 12 hours but survived and showed normal motor patterns for a further period of three weeks.

4. *Control of pH.*

Minor fluctuations in the pH of the serum/glucose medium were observed, but appeared to have no harmful effect on the worms. The use of phosphate buffers in the serum/Tyrode medium appeared to have no beneficial effect, but investigation is still proceeding.

5. *Determination of glycogen content of fresh and cultured worms.*

In view of the fact that addition of glucose appeared to be beneficial to the survival of *S. mansoni* worms *in vitro*, it was decided to investigate whether the reserves of glycogen decreased after a period *in vitro*, by determining the glycogen content of fresh and cultured worms. Bueding and Koletsky (1950) estimated the glycogen content of fresh *S. mansoni* worms, and found that in male worms glycogen constituted 14-29 per cent., and in females 3-5 per cent. of the dry weight. They also observed that the amount of glycogen in the males increased with the age of the worms.

Materials and methods.

Worms were obtained from the portal veins of hamsters 6-9 weeks after infection with *S. mansoni*. The worms were divided into two batches, one for culture and the other for estimation of glycogen. After a preliminary wash in saline, the surface moisture of the fresh or cultured worms was removed with absorbent paper, and the worms transferred to a tared tube and weighed. In one experiment, worms were maintained in Tyrode's solution, not horse serum/glucose, and after 65 hours were removed for estimation of their glycogen content.

The worm tissue was digested with alkali, and the glycogen precipitated with alcohol by the procedure of Heatley (1935) and estimated by the method of Boettiger (1946). Readings were taken on a Unicam spectrophotometer.

Results.

The results are given in Table I.

DISCUSSION.

Although the worms have not been kept in an environment exactly the same as that of the host, they do survive for up to two months *in vitro*. The present method, therefore, may safely be used for investigations on worms during the first few weeks of their life in a

serum medium. These cultures once set up, can be easily maintained without the difficulties so often associated with the culture of helminths *in vitro*, and make possible direct observations under reasonably uniform conditions, over a long period.

TABLE I.
Glycogen Content of Fresh and Cultured *Schistosoma mansoni*.

| Experiment No. | Weeks after infection of hamster before removal of worms | Sex of Worms | Days in Culture | Glycogen Content. Percentage of fresh weight |
|----------------|--|--------------|-----------------|--|
| 1. A. | 9 | M | — | 2.79 |
| B. | 9 | M | 10 | 2.5 |
| 2. A. | 7 | M | — | 3.8 |
| B. | 7 | M | 17 | 3.58 |
| 3. A. | 6 | M | — | 3.47 |
| B. | 6 | M | 10 | 3.85 |
| C. | 6 | M | * 2.7 | 3.4 |
| 4. A. | 7 | F | — | 0.9 |
| B. | 7 | F | 10 | 1.06 |
| 5. A. | 6 | F | — | 0.969 |
| B. | 6 | F | 14 | 0.895 |
| C. (i) | 6 | F | * 2.7 | 0.66 |
| (ii) | 6 | F | * 2.7 | 0.58 |

* Denotes cultures in which Tyrode's solution was used as a medium.

Physical factors have not yet been fully investigated, but the observations of Bueding, Peters and Waite (1947) show that decrease in oxygen tension has no effect on *S. mansoni*. In addition, small changes of pH and decreases in temperature have no observable effect and it seems that *S. mansoni* is rather insensitive to minor fluctuations in the environment, although further investigation along these lines is desirable.

Bueding (1951) found that *S. mansoni* utilizes in one hour an amount of carbohydrate equivalent to one-fifth of its dry weight, and it is thus probable that in the absence of carbohydrate from a medium, the reserve of glycogen would soon be exhausted. The close similarity between the glycogen content of cultured and fresh worms suggests that, *in vitro*, the worms do not rely on their reserves, but are absorbing carbohydrate from the medium. This view is borne out by the fact that the worms are noticeably more active in serum containing 0.1 per cent. added glucose than in medium to which no carbohydrate has been added.

From this evidence, therefore, it does not seem likely that the process of carbohydrate metabolism is seriously impaired when worms are removed from the host and maintained in a serum medium.

S. mansoni will only survive for a few days in Tyrode's solution and few conclusions can be drawn from the comparatively large amounts of glycogen still present in the worms maintained in Tyrode for 65 hours. The process of metabolism may cease after a few days in this medium, but certainly the inactivity of the worms could not be attributed to any lack of carbohydrate either in the medium or in the worm tissues.

The general activity and motor patterns of the worms, the frequency of copulation, the occurrence of egg laying, at least during the first few weeks *in vitro*, and the presence of an abundant carbohydrate reserve, all show that worms maintained *in vitro* by this method are living a reasonably normal life.

The method need not be confined to the culture of schistosomes, and other helminths could certainly be maintained in a similar way provided they were sterile when placed in the medium.

SUMMARY.

1. The method of maintaining schistosomes *in vitro* is described in detail.
2. Observations made on cultured *S. mansoni* are given.
3. Investigation of glycogen content shows that there is no significant difference between the reserve of glycogen in fresh and cultured worms. It is suggested that the worms do not rely on their reserve of glycogen but can take up carbohydrate from the medium.
4. The method could be adapted for the culture of other helminths besides schistosomes.

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On a Collection of Helminths from Thomson's Gazelle, *Gazella thomsoni*, from Tanganyika

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A collection of helminth parasites from Thomson's gazelle, *Gazella thomsoni*, was sent to the Department of Parasitology of the London School of Hygiene and Tropical Medicine for identification. They were collected by Mr. A. C. Brooks in Tanganyika from 1951–1954. Through the kindness of Professor J. J. C. Buckley, the material was placed at the writer's disposal for a detailed study.

The collection comprises one species of trematode, one species of a larval cestode, and eleven species of nematodes covering ten genera and four families. Of these nematodes, one is considered to be a new species and the other a new genus. Six genera of nematodes are recorded for the first time for the gazelle.

There are a number of scattered records of various parasites from gazelles, but no systematic study of its helminths have been made. It is the purpose of the present paper to describe this collection of helminths from Tanganyika, and to list together the various scattered records for this host.

TREMATODA.

The collection contained only one species of trematode.

Paramphistomidae Fiscoeder, 1901.

Paramphistomum Fiscoeder, 1901.

Paramphistomum microbothrium Fiscoeder, 1901.

This species was long considered a synonym of *Paramphistomum cervi* (Zeder, 1790) by the various writers who made revisions of the group. Näsmark (1937) redescribed it and showed its validity. Fiscoeder (1903) reported *P. microbothrium* from *Gazella dorcas*, while Ezzat (1945) reported *P. cervi* from *Gazella arabica*. Ezzat was unable

* L. S. Yeh. Part of a thesis approved by the University of London for the award of the Ph.D. degree.

to obtain the work of Näsmark and followed the classification of the older works. From his brief description, measurements and drawings, his material cannot be differentiated from the present material from Mkalama, Tanganyika.

The present collection appears to be *P. microbothrium* as redescribed by Näsmark. There are some slight differences, but our material is not very suitable for detailed histological study. Preserved specimens are short and stout, about 2.75 mm. in length; dorso-ventral 1.5. Dorsal line evenly curved. Posterior sucker 1.07 mm. in diameter. Its relation to body length 1 : 2.58, is of *Paramphistomum* type. Oesophagus 0.62 mm. Testes much flattened antero-posteriorly with very few lobes, measuring about 0.9 mm. dorso-ventrally and 0.93 mm. in height. In all specimens genital atrium contracted.

CESTODA.

Several larval cestodes all belonging to the same species were present in the material.

Cyclophyllidea.

Taeniidae Ludwig, 1886.

Taenia Linnaeus, 1758.

Taenia hydatigena Pallas, 1766 (Larva).

(*Cysticercus tenuicollis*).

A number of these larval cestodes were found free in the pleural cavity or attached to the omentum, the mesenteries and in one case encysted in the spinalis muscle. They came from Mkalama and Banagi, Tanganyika. The anatomy agrees with *Cysticercus tenuicollis*. Hall (1919) has listed *Gazella dorcas* as a host for this larval parasite.

NEMATODA.

Trichuridae Railliet, 1915.

Trichurinae Ransom, 1911.

Trichuris Roederer, 1761.

Trichuris spiricollis Solomon, 1932.

Solomon described this species from *Gazella thomsoni* from Naivasha, Kenya. Our material comes from Ngeta, Musoma Dist., Mto-wa-umbu, Sanya Plains and Banagi, Tanganyika.

Metastrongylidae Leiper, 1908.

Protostrongylus Kamensky, 1905.

Syn. *Synhetocaulus* Railliet and Henry, 1907.

Protostrongylus gazellæ sp. nov.

The lung of a gazelle was heavily parasitized by a number of these worms. They were massed in little clusters in the bronchioles at the tip of the lung. Unfortunately it was not possible to extract entire worms from the preserved material, but a fair number of cephalic and caudal extremities of both sexes were obtained. As they do not agree very well with any of the known species, a new name *Protostrongylus gazellæ* is proposed.

The length of the worms is unknown. The male has a diameter of about 0.10 mm. and the female 0.11 mm. The cuticle is smooth and without striations. The oesophagus is stout, short and gradually enlarges in diameter to its maximum in the posterior end. It measures 0.23–0.27 mm. in length and 0.042–0.046 mm. in maximum width in the males and 0.29–0.31 mm. in length and 0.048–0.058 mm. in width in the females. The nerve-ring is 0.10 mm. from the mouth in the male and 0.11 mm. in the female. The excretory pore and the very small cervical papillae are situated far posterior to the oesophagus, 0.41 mm. and 0.42 mm. in the male and 0.47 mm. and 0.49 mm. in the female.

Female: Tail short and terminates abruptly with a length of 0.08–0.10 mm. The vagina measures 0.67–0.72 mm. in length. The vulva is just anterior to the anus and 0.28 mm. from the tail end. The posterior lip of the vulva is much enlarged. Provagina present and provided with refractile globules in its posterior half. Eggs in vagina extremely thin-shelled with inconsistent shape making accurate measurement impossible, but are roughly 46×83 microns.

Male: Bursa typical of genus. Spicules in a number of specimens measure constantly 0.365 mm. in length. The small capitulum is triangular in shape with an arch cut in the inside and with three teeth projecting over it from the outside. Its structure resembles to some extent that seen in *Protostrongylus stilesi*. The paired corpus is lightly pigmented and measures about 0.075–0.079 mm. At the junction of the corpus and crura it appears lighter and refractile. The crura measures about the same length, 0.075–0.079 mm. and is stout, darkly pigmented and hooked at the tip. It has a well-developed ala. The paired crura are separated structures. The telamon is unpigmented

and not easily discernible. It appears to agree in general structure with that given for *P. raillieti* by Schulz *et al.*

Discussion: This species resembles *Protostrongylus rupicaprae* rather closely but has several differences, the main differences being the much larger spicule and the difference of structure of the capitulum which appears rather marked. For this reason we consider this species apart and propose the name *Protostrongylus gazellae*.

Specific diagnosis: Metastrongylidae Leiper, 1908. *Protostrongylus* with characters of genus. Length unknown. Oesophagus 0.23–0.27 \times 0.042–0.046 mm. in male and 0.29–0.31 \times 0.048–0.058 mm. in female. Nerve-ring 0.10 mm. and 0.11 mm. in male and female respectively. Excretory pore and cervical papillae posterior to oesophagus and 0.41 mm. and 0.42 mm. respectively in the male and 0.47 mm. and 0.49 mm. in the female. *Female:* Tail 0.08–0.10 mm. Vagina 0.67–0.72 mm. long. Vulva 0.28 mm. from tail end. Posterior lip of vulva enlarged. Provagina present. Eggs thin-shelled measuring about 46 \times 83 microns. *Male:* Bursa typical of genus. Spicule 0.365 mm. in length. Capitulum triangular with arch cut on inside and three projecting teeth. Corpus lightly pigmented and measures 0.075–0.079 mm. Crura with same length as corpus, stout, deeply pigmented and hooked at tip. The paired structures not fused. Telamon similar to general structure of *P. raillieti*.

Host: *Gazella thomsoni*.

Location: Bronchioles.

Type locality: Mkalama, Singida District, Central Province, Tanganyika.

Co-types: Deposited in the Department of Parasitology, London School of Hygiene and Tropical Medicine.

Trichostrongylidae Leiper, 1912.

Trichostrongylus Looss, 1905.

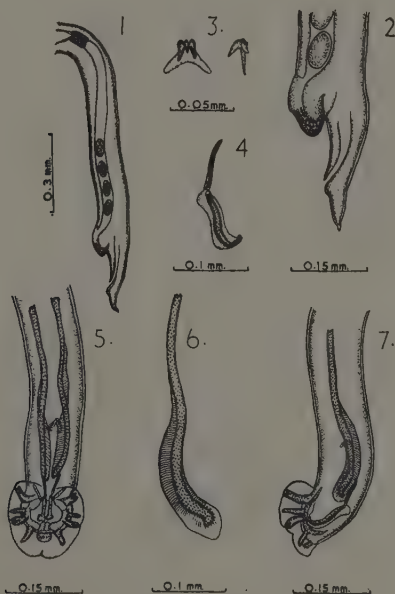
Trichostrongylus probolurus (Railliet, 1896) Looss, 1905.

This well-known cosmopolitan parasite from the ruminant has been reported from *Gazella dorcas* from North Africa by Neveu-Lemaire (1918) and also *Gazella thomsoni* (quoted from Neveu-Lemaire, 1936, p. 989). Our material comes from Banagi and Loliondo, Tanganyika.

Haemonchus Cobb, 1898.

Haemonchus contortus (Rudolphi, 1803) Cobb, 1898.

This parasite has been reported by Gebauer (1982) from *Gazella rufifrons* in Austria, and Ezzat (1945) from *G. rufifrons* from Sengambia, Nigeria and Sudan. Our material comes from Mto-wa-mbu, Banagi and Eyasi, Tanganyika.



Protostrongylus gazellae sp. nov.

Fig. 1.—Posterior part of female. Fig. 2.—Tail extremity of female.

Fig. 3.—Capitulum. Fig. 4.—Corpus and crura.

Fig. 5.—Ventral aspect of male. Fig. 6.—Spicule.

Fig. 7.—Lateral aspect of male.

Longistrongylus Leroux, 1931.

Longistrongylus meyeri Leroux, 1931.

A number of these trichostrongylids were found in the abomasum of gazelles. In one it was a pure infection, while the other a multiple

infection with *Haemonchus contortus* and *Trichostrongylus probolurus*. They all came from Banagi, Tanganyika.

Leroux (1931) described these worms from a red harbeest, *Bubalis caama* from Gobalis in South West Africa. Our specimens are very much smaller and thinner than those in the original description.

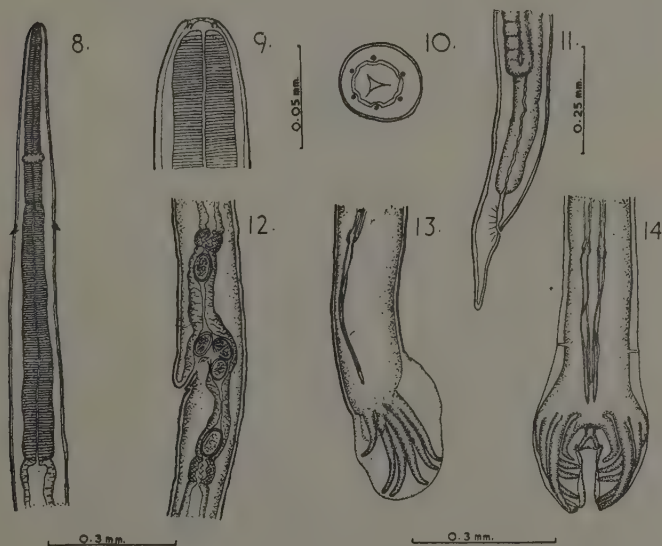
TABLE I.
Dimensions of *Longistrongylus meyeri* from Hartebeest and Gazelle.

| | Hartebeest LeRoux, 1931 | | Gazelle Yeh Liang-Sheng | |
|--------------------------------------|----------------------------|-------------|----------------------------|-----------|
| | Female | Male | Female | Male |
| Length of body | 24.5-27.3 | 14.4-15.8 | 12.2-13.4 | 10.5-10.7 |
| Width | 0.375-0.437 | 0.247-0.263 | 0.13-0.16 | 0.11-0.12 |
| Length of oesophagus .. | 1.362-1.652 | 1.212-1.218 | 1.00-1.10 | 0.89-0.97 |
| Nerve-ring to anterior end .. | 0.425-0.463 | 0.336-0.357 | 0.29-0.37 | 0.30-0.32 |
| Excretory pore to anterior end .. | 0.653-0.764 | 0.454-0.516 | 0.42-0.53 | 0.44 |
| Cervical papillae to anterior end .. | 0.674-0.735 | 0.486-0.547 | 0.46-0.55 | 0.45-0.47 |
| Vulva from posterior end .. | 3.838-5.827 | — | 2.6-3.0 | — |
| Eggs | 0.075-0.077 | — | 0.065-0.074 | — |
| | x 0.045-0.048 | | x 0.044-0.050 | |
| Tail | 0.243-0.252 | — | 0.16-0.20 | — |
| Spicule | — | 0.300-0.312 | — | 0.33-0.35 |

The author had the opportunity of studying some of the holotype and paratypes deposited in the Department of Parasitology of the London School of Hygiene and Tropical Medicine, and believes that the present material belongs to the same species. As the ample material differs from that of the types in some respects, a redescription of the gazelle material is given. This genus and species is a new host record.

These are fair-sized worms measuring 10.5-10.7 mm. by 0.11-0.12 mm. in the males and 12.2-13.4 mm. by 0.13-0.16 mm. in the females. The cuticle has very fine transverse striations and about 38 coarse longitudinal ridges. The anterior end attenuates gradually and without cephalic cuticular dilation. The head has three rudimentary

lips. There is a circle of six papillae. Buccal cavity small. The oesophagus measures 0.89–0.97 mm. in the male and 1.00–1.10 mm. in the female. There is a slight difference in histological texture in the oesophagus suggesting muscular and glandular parts, but the difference is not marked. Nerve-ring and excretory pore 0.80–0.82 mm. and 0.44 mm. respectively in the male, and 0.29–0.87 mm. and 0.42–0.52 mm. in the female. The cervical papillae are fairly large, pointing posteriorly and situated 0.45–0.47 mm. from the anterior end in the male and 0.46–0.55 mm. in the female.



Longistrongylus meyeri.

Fig. 8.—Anterior end. Fig. 9.—Head end.

Fig. 10.—End-on view of head. Fig. 11.—Posterior end of female.

Fig. 12.—Vulval region. Fig. 13.—Lateral aspect of male tail.

Fig. 14.—Dorsal aspect of male tail.

Female: The caudal end tapers to a cone-shaped tail measuring 0.16–0.20 mm. The vulva is situated at a distance of one-quarter of the length from the posterior end, or 2.6–3.0 mm. from the tail, and divides the worm in a ratio 3.2–4.0. In Leroux's material the vulva

is depressed. In the present gazelle material the vulval lips are found to be very variable as it may be depressed or have a small anterior lip as shown in the drawing. The vagina is short. The ovejectors and uteri are divergent. The eggs are ovoid, thick-shelled and measure 65–74 by 44–50 microns.

Male: Spicules are equal, simple and slender, but not filiform. They measure 0.83–0.85 mm. in length. The distal ends are pointed, but prior to their termination there is a small wing. The extremity is entire and not split. There is no gubernaculum. Telamon ill-defined. Pre-bursal papillae present. Bursa as in genus.

Host: *Gazella thomsoni*.

Location: Abomasum.

Locality: Banagi, Tanganyika.

Cooperioides antidorca (Mönnig, 1981).

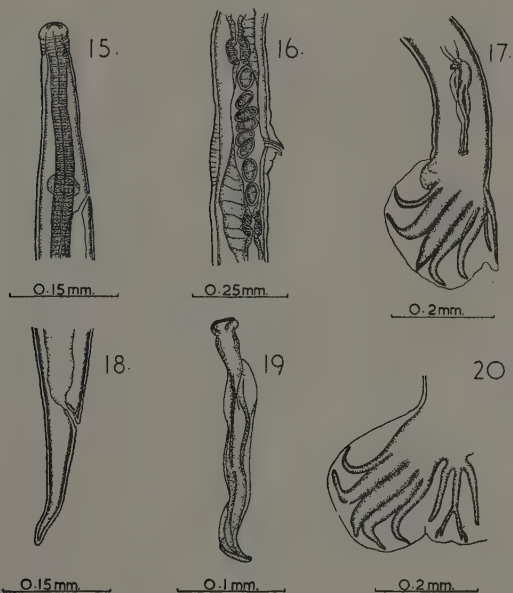
These specimens were found either encapsulated or free in the wall of the duodenum of gazelles from Loliondo and Banagi, Tanganyika. This is a new host record for this genus and species.

The worm is attenuated anteriorly and has its thicker portion at the posterior half. The males measure 4.7–6.7 mm. in length and 0.12–0.18 mm. in width and the females measure 7.0–8.4 mm. by 0.11–0.18 mm. The cuticle has fine transverse striations and ten longitudinal ridges. The cuticle of the head is slightly dilated with transverse striations on the posterior half. The head has a diameter of about 0.034–0.046 mm. in both sexes. The oesophagus is 0.39–0.46 mm. in the male and 0.46–0.52 mm. in the female. The excretory pore and nerve-ring are 0.21–0.23 mm. and 0.14–0.20 mm. respectively in the male and 0.21–0.25 mm. and 0.20–0.26 mm. in the female.

Female: The tail is long and pointed measuring 0.15–0.19 mm. in length. The vulva is in the posterior half of the worm, 1.50–1.96 mm. from the caudal end. It is only seldom surrounded by a thickening of the cuticle as noted by Mönnig, but all our specimens have a pair of very conspicuous projections resembling the cerci of a grasshopper. The combined length of the ovejectors is 0.44–0.54 mm. The thick-shelled, ovoid eggs were in the two cell stage and measure 46×67 –71 microns.

Male: The bursal rays are as figured. The spicules are 0.206–0.220 mm. in length and have a number of folds and alae. The specimens

agree very well with the description given by Mönnig with the exception that at the distal tip there is a very distinct foot lying in-between the two alae; otherwise the folds, ridges and alae appear to be identical. There is no gubernaculum or telamon.



Cooperioides antidorca.

Fig. 15.—Anterior end. Fig. 16.—Vulval region.

Fig. 17.—Lateral aspect of male tail. Fig. 18.—Female tail.

Fig. 19.—Spicule. Fig. 20.—Bursa.

Discussion: The specimens agree very well with Mönnig's description with the exception of two important points. First, in the female the vulva terminates in a pair of conspicuous cerci and not merely thickenings of the cuticle as stated by Mönnig. Secondly, the spicule in the male has a distinct foot between the two alae at the distal end, which is not described or figured by Mönnig. It appears that the latter author either overlooked these characters, or our specimens represent

a variation in the species.

Host: *Gazella thomsoni*.

Location: Duodenum.

Locality: Loliondo and Banagi, Tanganyika.

Paracooperia serrata (Mönnig, 1981) Travassos, 1985.

A female gazelle from Loliondo harboured five species of trichostrongylid nematodes in its duodenum, and among these, two species belonged to the genus *Paracooperia*, namely *Paracooperia serrata* and *Paracooperia daubneyi*. The males of these two species were very easily separated by the shape of the spicules. The females, however, could not be separated into two groups as they all appeared very much alike in size and had the long linguiform process over the vulva. For this reason, only the male specimens will be described for this species.

These small nematodes measure 4.2–4.5 mm. in length and 0.09–0.10 mm. in width. The cuticle of the head is slightly dilated to give a head diameter of about 0.033 mm. The oesophagus is 0.91–0.93 mm. in length being slightly thicker in the posterior than the anterior end. The excretory pore and nerve-ring are situated 0.19–0.21 and 0.17–0.20 mm. respectively from the cephalic extremity. The bursal rays agree very well with the genus. The spicules measure 0.230–0.246 mm. in length. Each has a strong medial arm separated from the rest of the body and with wavy serrations giving an appearance of 5–7 teeth. The large and small serrations alternate, so that looking from the side, they appear as a number of sharp teeth. Median to the serrations, there is a long spike, giving the spicule a trifurcate appearance. Distally on the main body there is a foot pointing medially and set almost at a right angle. At the extreme distal extremity there is a thick highly refractile "shoe."

Discussion: The species *Paracooperia serrata* was erected by Mönnig from the small intestine of the Springbok, *Antidorca marsupialis* from South Africa. The spicule has 4–5 "dentate processes." Daubney (1933) redescribed and figured what he believed to be this species from the small intestine of *Ovis aries* from the Rift Valley and Athi Plains, Kenya. His material had seven teeth. Travassos (1987) believed Daubney's description as different from *P. serrata* and accordingly named it *P. daubneyi*. Our present findings are in agreement with those of Travassos.

Paracooperia daubneyi Travassos, 1937.

The abomasum and jejunum of several gazelles from Banagi and Loliondo, Tanganyika, harboured this parasite.

These worms' measurements are 6.1–7.3 mm. in length by 0.08–0.14 mm. in width in the males and 6.5–6.8 mm. by 0.09–0.11 mm. in the females. They taper only slightly in the anterior part. The whole body has faint transverse cuticular striations. In the cephalic region there is a slight collar-like cuticular inflation measuring about 0.033–0.043 mm. across. The nerve-ring is situated about 0.17–0.23 mm. from the anterior end; the excretory pore is 0.22–0.28 mm. and

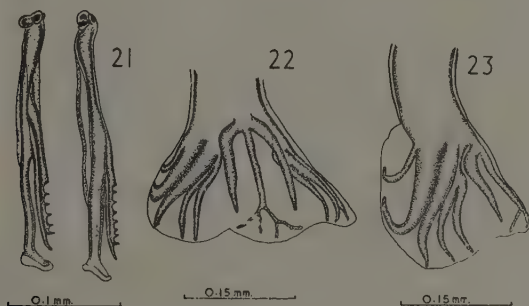
*Paracooperia serrata*.

Fig. 21.—Spicules. Fig. 22.—Dorsal aspect of bursa.

Fig. 23.—Lateral aspect of bursa.

the cervical papillae are 0.25 mm. distant from it. The oesophagus has a length of 0.40–0.43 mm. with a maximum diameter of 0.022 mm. The buccal capsule is inconspicuous, circular and terminal. There appear to be six rudimentary lips. In the spaces between the rudimentary lips there are noticed six pairs of reduced papillae. In the external circle only four large simple papillae were observed.

Female: The tail measures 0.13–0.15 mm. in length, and attenuates gradually to a fine point. The vulva is situated 1.3–1.4 mm. from the caudal extremity. It has a prominent posteriorly directed linguiform process joined to the anterior lip measuring about 0.13–0.15 mm. in length. Vagina short and directed anteriorly. Ovejectors and uteri divergent, 0.62 mm. in length. The ovoid eggs measure $38\text{--}44 \times 58\text{--}65$ microns.

Male: The bursal rays are typical of the genus. Parts of the inner surface are ornamented with small bosses. Prebursal papillae present. Spicules measure 0.288–0.310 mm. in length and are trifurcate, i.e. the equivalent of the spike as seen in *Paracooperia serrata* is conspicuous and very well developed here. The serrated part of the spicule gave it the appearance of having 8–10 teeth. The teeth start about 0.145–0.167 mm. from the anterior end of the spicule and continue for about 0.085–0.10 mm. This gives a ratio of serrations to length of spicule as 1 : 2.1. The genital cone is large and pointed. Gubernaculum and telamon absent.

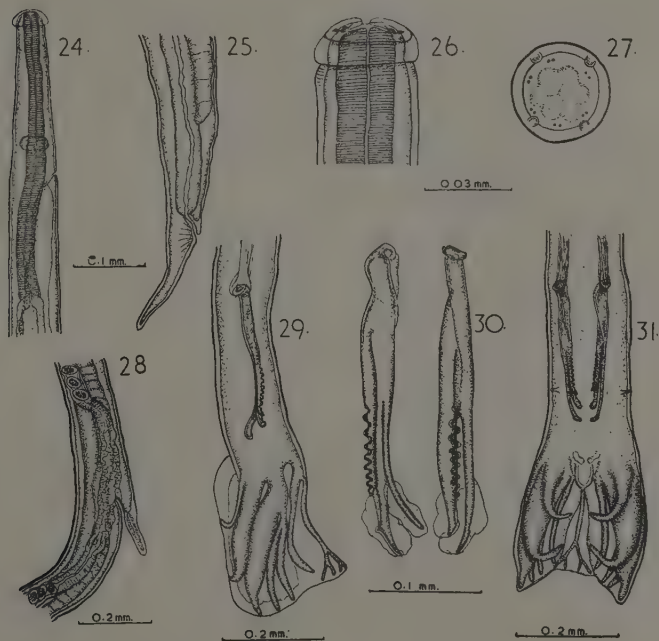
Discussion: *Paracooperia serrata* and *P. daubneyi* constitute new host records for the gazelle. The serrations of the spicule were variously described as teeth or dentations. Actually they are neither dentations nor teeth as pointed out by LeRoux (1950) but a chitinous ridge waving in a dorso-ventral aspect. The shape of the distal end of the spicule makes it easy to differentiate *P. serrata* and *P. daubneyi*.

Gazellostrongylus lerouxi gen. et sp. nov.

Several of these worms were collected either free or from nodules in the abomasum of gazelles from Loliondo and Mkalama, Tanganyika. As many as fifteen specimens have been found in a single nodule. One male and two females were in a fair state of preservation but stained with tannin, while some thirty or forty specimens in a number of other tubes were macerated from late fixation or bad preservation. As the general morphology is unlike any of the known genera in the family, it is placed in a new genus, and the name *Gazellostrongylus lerouxi* is proposed in honour of Dr. P. L. Leroux for his valuable contributions to our knowledge of this family.

These worms are comparatively large and stout. The males measure 20–30.5 mm. in length by 0.43–0.48 mm. in width, while the females measure 38.5–48 mm. and 0.51–0.62 mm. respectively. The anterior end terminates very abruptly making the region around the oesophagus appear much blown-out. The posterior end in the female tapers gradually. The cuticle has fine transverse striations and coarse longitudinal thickenings of about 0.001 mm. and 0.1 mm. apart respectively. The cephalic end has a slight cuticular swelling with the striations dividing it into two parts. As the anterior part of the worm enlarges so rapidly towards the posterior, this slight cephalic swelling is very inconspicuous.

The head diameter is 0.087–0.096 mm. in the male and 0.010–0.011 mm. in the female. The mouth has six lips. Buccal capsule absent. External circle of four papillae. Oesophagus straight and short. It is uniform in thickness except for the posterior part which enlarges slightly and then narrows down again at the end. It measures 0.54–0.67 mm. in length in the male and 0.73–0.85 mm. in the female. The anterior



Paracooperia daubneyi.

Fig. 24.—Anterior end of worm. Fig. 25.—Posterior end of female. Fig. 26.—Head end of worm. Fig. 27.—Head, end-on view. Fig. 28.—Vulval region. Fig. 29.—Lateral view of bursa. Fig. 30.—Spicules. Fig. 31.—Ventral view of bursa.

average diameter is 0.067–0.075 mm. and the posterior maximum diameter 0.083–0.092 mm. in the male and 0.075–0.079 mm. and 0.096–0.108 mm. respectively in the female. Small cervical papillae are present, 0.27–0.36 mm. from the anterior end in the male, but could not be clearly seen in the female. The excretory pore and nerve

ring are 0.23–0.28 mm. and 0.16–0.25 mm. in the male and 0.25–0.82 mm. and 0.25–0.80 mm. respectively in the female.

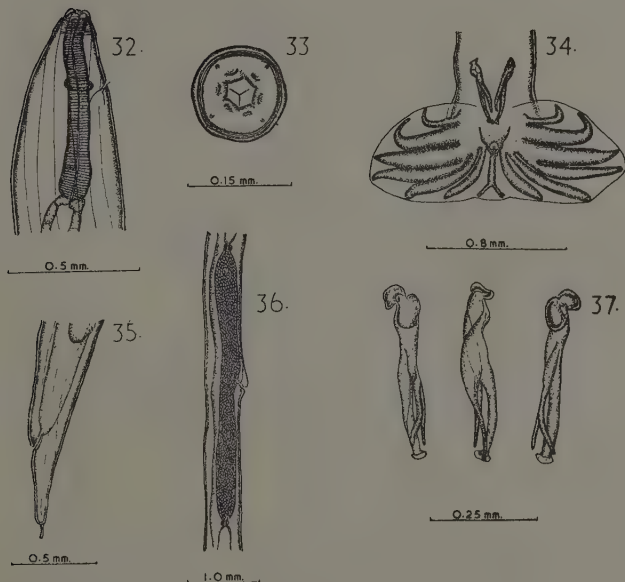
Female: The vulva is situated 10.0–11.6 mm. from the posterior tip. It has a transverse slit and inconspicuous lips. Vagina short. Ovejectors and uteri opposed. Long ovejectors with a combined length of about 3.7 mm. Eggs oval and thin-walled, measure *in utero* 46–50 by 66–83 microns. Tail 0.46–0.57 mm. and tapers gradually to end in a terminal spike 0.04–0.06 mm. long.

Male: The bursa has extremely well-developed lateral rays. The ventral rays arises from a common trunk. Ventro-ventral small, latero-ventral much larger with tip directed ventrad but do not meet. Externo-lateral and medio-lateral from common trunk, large and parallel. Postero-lateral slightly smaller, independent in origin and close to other laterals. Externo-dorsal fairly large, with origin at base of dorsal ray. Dorsal ray bifurcate near tip and each extremity bidigitate. Genital cone conical and pointed. Prebursal papillae not observed. Spicules equal, similar, stout, short and trifurcate. They measure 0.416–0.445 mm. in length. There are no alae. The main branch ends with an unpigmented shoe. Gubernaculum absent, telamon present.

Discussion: The species described above does not resemble any of the known species in the family Trichostrongylidae. The new genus shows close affinity to the genus *Cooperioides* Daubney, 1933. It differs in many important points. The cephalic end is very different as it tapers abruptly and the mouth has six lips; the oesophagus is short and slightly bulbous in the posterior part. The spicule is distinctly trifurcate and unlike that found in *Cooperioides*. The bursal rays are very different from the genotype *Cooperioides kenyensis* Daubney, 1933. Most noteworthy are the ventral rays in *Gazellostrongylus* which are very unequal. Ventral and lateral rays are closely placed and well developed, while the dorsal rays are comparatively short with a different shape and pattern from those of *Cooperioides*. Because of the larger lateral rays and the shorter dorsal rays, in fixed specimens the bursa tends to open out like a bi-valve mollusc and very easily spread-out for study. This is not so with *Cooperioides*.

Generic diagnosis: Trichostrongylidae Leiper, 1912. Trichostrongylinae Leiper, 1908. Cuticle with fine transverse striations and coarse longitudinal ridges. Cephalic end of worm narrows abruptly. Mouth with six lips. Little or no cephalic swelling. Cephalic end divided

into two by the distinct transverse striations, making the lips look more conspicuous. Small cervical papillae present. Vulva in middle of posterior half of worm. Ovejectors and uteri divergent. Tail of female tapers gradually and may end in a single spike. Bursa with stout, long



Gazellostrongylus lerouxi gen. et sp. nov.

Fig. 32.—Anterior end. Fig. 33.—End-on view of head.

Fig. 34.—Ventral aspect of male tail. Fig. 35.—Female tail.

Fig. 36.—Vulval region. Fig. 37.—Spicules.

and closely packed lateral rays and comparatively short dorsal rays. Ventro-ventral much smaller than latero-ventral, separated from each other and with their tips directed anteriad but not meeting. Laterals stout and almost parallel. Externo-dorsal large and arises from base of dorsal. Dorsal ray bifurcates at extremity and each fork is

bidigitate. Spicules short and equal, usually trifurcate. Gubernaculum absent, telamon present.

Parasite of ruminants.

Genotype: *Gazellostrongylus lerouxi* sp. nov.

Specific diagnosis: Trichostrongylinae Leiper, 1908 with generic characters. Medium sized worms about 20–30 mm. in length by 0.43–0.48 mm. in width for the males and 38–48 mm. by 0.54–0.62 mm. for the females. Mouth with six lips. Transverse cuticular striations and longitudinal ridges 0.001 mm. and 0.1 mm. apart respectively. Oesophagus short, 0.54–0.67 mm. in length in the male and 0.73–0.85 mm. in female, with maximum diameter in posterior part. Cervical papillae small, 0.27–0.35 mm. from anterior end in male. Vulva 10–11.6 mm. from posterior tip with non-protuberant lips. Ovejectors and uteri opposed. Combined length of ovejectors 3.7 mm. Tail conical, 0.46–0.57 mm. in length. Eggs oval, thin-walled, measuring 45–50 by 66–83 microns. Bursa with small ventro-ventral and large latero-ventral with tips directed anteriorly but do not meet. Lateral rays large and well-developed, almost parallel. Externo-lateral and medio-lateral with common origin. Externo-dorsal much smaller than laterals with origin at base of dorsal. Dorsal bifurcates at tip and each fork is bidigitate. Spicules similar, short, stout, with trifurcate tips and 0.416–0.445 mm. in length. Main branch with unpigmented shoe. Gubernaculum absent, telamon present.

Host: *Gazella thomsoni*.

Location: Abomasum.

Type locality: Loliondo, Northern Province, Tanganyika.

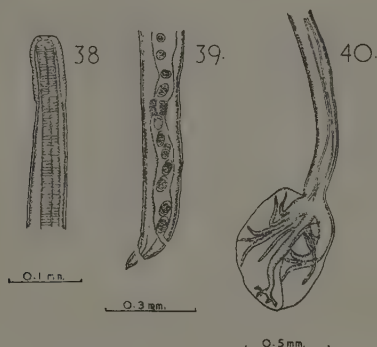
Type: Deposited in the Department of Parasitology, London School of Hygiene and Tropical Medicine.

Paratypes: Large numbers of macerated specimens also deposited in above Institution.

Impalaia nudicollis Mönnig, 1931.

This species was described by Mönnig from the small intestine of the Blesbuck, *Damaliscus albifrons*, from South Africa. Daubney (1933) recorded it from the fourth stomach and small intestine of *Ovis aries* from Mpapwa, Tanganyika; Rift Valley and Athi Plains, Kenya.

In the present collection there were a number of specimens of this species in gazelles from Loliondo and Banagi, Tanganyika. This is the first record of this genus and species in *Gazella*. Daubney is of the opinion that the sheep is not the normal host of this nematode, and that it probably belongs to some game animal. This species was present in two gazelles out of twenty-six from different parts of Tanganyika.



Impalaia nudicollis.

Fig. 38.—Anterior end. Fig. 39.—Posterior end of female.

Fig. 40.—Posterior end of male.

The worm is generally attenuated towards the anterior, but the head is dilated. The cuticle has fine transverse striations and longitudinal ridges. The male measures 6.2–8.2 mm. in length by 0.12–0.13 mm. in width; and the female 14.6–15.3 mm. in length and 0.13–0.15 mm. in width. The head has a diameter of about 0.04–0.05 mm. and the head cuticle is inflated for a length of 0.06–0.10 mm. and is without tubercles. The mouth is surrounded by three small lips and six papillae. The oesophagus is 0.38–0.43 mm. in the male and 0.40–0.49 mm. in the female. It appears to have two parts but the division is not very marked. The excretory pore is 0.33–0.44 from the anterior end in both sexes.

Female: The female broadens posteriorly to the vulva, which is situated near the caudal extremity about 0.17–0.22 mm. from the tail end. The caudal extremity narrows abruptly to form a conical tail 0.054–0.063 mm. long. The uterus and ovejector are 0.5–0.6 mm. in length. The eggs measure $67\text{--}73 \times 38\text{--}44$ microns.

Male: The bursa is long and voluminous. The general pattern of the rays agree very well with the genotype, *Impalaia tuberculata* Mönnig, 1924. The bursa has a net-work structure resembling the veins of the insect wing. The dorsal ray is extremely long and measures about 0.44 mm. The alated filiform spicules measure 0.835–1.16 mm. in length, and end in a single point. The small gubernaculum measures 0.09–0.10 mm. long.

In the present specimens the excretory pore is large and distinct, but neither Mönnig nor Daubney observed it.

Host: *Gazella thomsoni*.

Location: Duodenum.

Locality: Loliondo and Banagi, Tanganyika.

Filariidae (Cobbold, 1864) Claus, 1885.

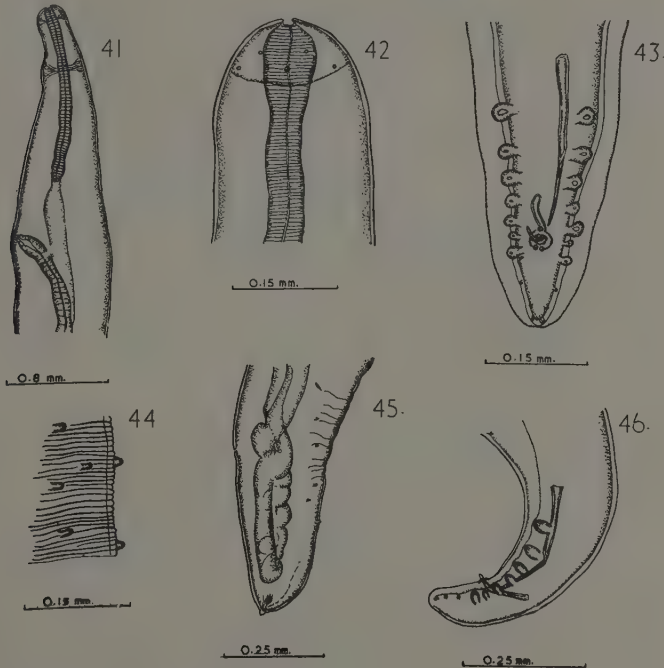
Gazellofilaria Yeh Liang-Sheng, 1955.

Gazellofilaria tanganyikae Yeh Liang-Sheng, 1955.

One entire female of this species and several damaged specimens and fragments of both sexes were present in the collection. It was demonstrated at a Laboratory Meeting of the Royal Society of Tropical Medicine and Hygiene (Yeh Liang-Sheng, 1955). This is the first record of a filariid worm from the gazelle.

Female: The undamaged female specimen measures 175 mm. in length and 0.53 mm. in width. Anteriorly the worm attenuates from the vulva onwards, while posteriorly it narrows down gradually. The cuticle has fine transverse striations, a pair of parallel longitudinal ridges on each lateral aspect and a large number of bosses. The cuticular bosses are large and prominent and begin to become numerous at 15 mm. from the cephalic end and continue to the caudal end. There are ten head papillae arranged in the usual filariid manner. The oesophagus is 1.8 mm. in length. Its anterior part is surrounded by a chitinous ring. The gut is a slender tube. The anus is an inconspicuous opening 0.44 mm. from the posterior extremity. The tail ends in three papilla-like structures, one central and caudal and the others lateral. The dorsal lateral longitudinal ridges increase slightly in height in the caudal region to appear as rudimentary caudal alae. The ventral longitudinal ridge joins the dorsal ridge at the lateral

caudal papilla-like structure. The excretory pore is 0.54 mm. from the mouth end. The vulva opens 1.78 mm. from the anterior. The uterine coils can be seen in the post-anal region. Microfilariae present in pre-vaginal uterus.



Gaselofilaria tanganyikae.

Fig. 41.—Anterior end. Fig. 42.—Head.

Fig. 43.—Ventral aspect of male tail. Fig. 44.—Cuticle showing bosses.

Fig. 45.—Female tail. Fig. 46.—Lateral aspect of male tail.

Male: The alate male tail is coiled. The shorter right spicule measures 0.125 mm. in length. The left spicule is much longer and measures 0.259 mm. in length. About half-way in its length it has a twist and bend and immediately slenders down considerably. The caudal papillae are as figured. Laterally there are seven pairs of large papillae, five of which are pre-cloacal, one ad-cloacal, and another post-cloacal. Continuing in the lateral post-cloacal region there are three to

five very small papillae of which the last two pairs on each side appear to be fused. On the ventral aspect there is a single small papilla immediately in front of the cloacal opening and a pair close behind it. The cloaca is 0.11 mm. from the tail end.

Discussion: The genus *Gazellofilaria* Yeh Liang-Sheng, 1955 closely resembles the genera *Loa* and *Dirofilaria*. The most important difference in *Dirofilaria* is that the cuticle is smooth whereas in *Gazellofilaria* the cuticle throughout almost the entire body is covered with large bosses. The species *Gazellofilaria tanganyikae* appears to be closely related to *Dirofilaria asymmetrica* Kreis, 1938. LeRoux (personal communication) believes that *Dirofilaria asymmetrica* Kreis, 1938 and *Dirofilaria kuelzii* (Rodenwaldt, 1910) do not belong to the genus *Dirofilaria* and are probably members of *Gazellofilaria*. A comparison of *Gazellofilaria tanganyikae* shows it to be very closely related to *Dirofilaria asymmetrica*, but as Kreis makes no mention of any gross bosses, I describe the present material as new. If on re-examination, the cuticle of *D. asymmetrica* proves to have gross bosses, then *Gazellofilaria tanganyikae* should be a synonym of *Gazellofilaria asymmetrica* (Kreis, 1938).

Genotype: *Gazellofilaria tanganyikae*.

Type host: *Gazella thomsoni*.

Location: Peritoneal cavity and mesentery.

Type locality: Loliondo, Northern Province, Tanganyika.

Types: Deposited in the Department of Parasitology, London School of Hygiene and Tropical Medicine.

CHECK LIST OF HELMINTHS OF GAZELLES.

TREMATODA.

Paramphistomidae Fischöder, 1901.

Paramphistomum Fischöder, 1901.

Paramphistomum cervi (Zeder, 1790).

G. arabica

Ezzat, 1945, p. 16.

Paramphistomum microbothrium Fischöder, 1901.

G. dorcas N. Africa

Fischöder, 1903, p. 535-8.

G. dorcas

Näsmark, 1937, p. 450-2.

G. thomsoni Tanganyika

Yeh Liang-Sheng,
present paper.

Dicrocoeliidae (Looss, 1907) Odhner, 1910.

Dicrocoelium (Dujardin, 1845) E. Blanchard, 1847.

Dicrocoelium dendriticum (Rudolphi, 1819) Looss, 1899.

G. dorcas ——— Travassos, cited 1944,
p. 30-7.

CESTODA.

Taeniidae Ludwig, 1886.

Taenia Linnaeus, 1758, s. str.

Taenia hydatigena Pallas, 1766 (Larval stage)
(*Cysticercus tenuicollis*).

G. dorcas ——— Hall, cited 1919, p. 31.

G. thomsoni Tanganyika Yeh Liang-Sheng,
present paper.

Multiceps Goeze, 1782.

Multiceps multiceps (Leske, 1780) Hall, 1910 (Larval stage).

Gazella sp. ——— Hall, cited 1919, p. 43.

Anoplocephalidae Cholodkovsky, 1902,
emended Fuhrmann, 1907.

Moniezia Blanchard, 1891.

Moniezia expansa (Rudolphi, 1810).

Gazella sp. ——— Spina, 1935, p. 21.

Avitellina Gough, 1911.

Avitellina centripunctata (Rivolta, 1874).

G. granti Abyssinia Fuhrmann and Baer, 1944,
p. 119.

Stilesia Railliet, 1893.

Stilesia globipunctata (Rivolta, 1874).

G. granti Abyssinia Fuhrmann and Baer, 1944,
p. 119.

NEMATODA.

Trichuridae Railliet, 1915.

Trichuris Roederer, 1761.

Trichuris gazellae Gebauer, 1933.

**G. dama* Schönbrunn Zoo, Gebauer, 1933, p. 323.
Austria

Gazella sp. Unknown Ezzat, 1945, p. 33-34.

Trichuris globulosa (v. Linstow, 1901) Ransom, 1911.

G. albonotata Egypt Ezzat, 1945, p. 31-2.

G. dama

G. dorca

G. leptoceros

G. rufifrons

Trichuris ovis (Abilgaard, 1795) Smith, 1908.

G. dama Schönbrunn Zoo, Gebauer, 1933, p. 323.
Austria

G. albonotata Egypt Ezzat, 1945, p. 28-29.

G. dama

G. dorcas

G. leptoceros.

G. rufifrons

G. soemmerringi

Trichuris spiricollis Solomon, 1932.

G. thomsoni Kenya Solomon, 1932, p. 218.

G. thomsoni Tanganyika Yeh Liang-Sheng,
present paper.

Oxyuridae Cobbold, 1864.

Skrjabinema Wereschtschagin, 1926.

Skrjabinema ovis (Skrjabin, 1915).

G. subgutturosa Russi Schulz, 1928, p. 102-8.

Strongylidae Baird, 1853.

Chabertia Railliet and Henry, 1909.

Chabertia ovina (Gmelin, 1790) Railliet and Henry, 1909.

G. dorcas Austria Gebauer, 1932, p. 167.

Oesophagostomum Molin, 1861.

Oesophagostomum (*Hudsonia*) *walkeri* Mönnig, 1932.

G. thomsoni Tanganyika Leroux, 1940, p. 7, 9, 10.

Metastrongylidae Leiper, 1908.

Dictyocaulus Railliet and Henry, 1907.

*This check list of helminths for *Gazella dama* does not include those reported under *Cervus dama* or *Dama dama*.

Dictyocaulus filaria (Rudolphi, 1809).

Gazella sp. ———

Neveu-Lemaire, cited 1918,
p. 12.

Protostrongylus Kamensky, 1905.

Protostrongylus gazellae sp. nov.

G. thomsoni Tanganyika

Yeh Liang-Sheng,
present paper.

Trichostrongylidae Leiper, 1908.

Trichostrongylus Looss, 1905.

Trichostrongylus colubriiformis (Giles, 1892) Ransom, 1911.

G. dorcas N. Africa

Neveu-Lemaire, 1918, p. 18.

G. dama Schönbrunn Zoo,
Austria

Gebauer, 1933, p. 323.

Trichostrongylus probolurus (Railliet, 1896) Looss, 1905.

G. dorcas N. Africa

Neveu-Lemaire, 1918, p. 18.

G. thomsoni ———

Neveu-Lemaire, cited 1936,
p. 989.

G. thomsoni Tanganyika

Yeh Liang-Sheng,
present paper.

Haemonchus Cobb, 1898.

Haemonchus contortus (Rudolphi, 1803) Cobb, 1898.

G. rufifrons Austria (Zoo)

Gebauer, 1932, p. 171.

G. rufifrons Sengambia
Nigeria
Sudan

Ezzat, 1945, p. 53-56.

G. thomsoni Tanganyika

Yeh Liang-Sheng,
present paper.

Camelostrongylus Orloff, 1933.

Camelostrongylus mentulatus (Railliet and Henry, 1909) Orloff, 1933.

G. dama Schönbrunn Zoo,
Austria

Gebauer, 1933, p. 323.

G. bennetti India

Sarwar, 1945, p. 274.

Nematodirus Ransom, 1907.

Nematodirus spathiger (Railliet, 1896),

G. subgutturosa Russia

Schulz, 1928, p. 101.

Impalaia Mönnig, 1924.

Impalaia nudicollis Mönnig, 1931.

G. thomsoni Tanganyika Yeh Liang-Sheng,
present paper.

Longistrongylus Leroux, 1931.

Longistrongylus meyeri Leroux, 1931.

G. thomsoni Tanganyika Yeh Liang-Sheng,
present paper.

Cooperioides Daubney, 1933.

Cooperioides antidorca (Mönnig, 1931) Daubney, 1933.

G. thomsoni Tanganyika Yeh Liang-Sheng,
present paper.

Paracooperia Travassos, 1935.

Paracooperia serrata (Mönnig, 1931) Travassos, 1935.

G. thomsoni Tanganyika Yeh Liang-Sheng,
present paper.

Paracooperia daubneyi Travassos, 1937.

G. thomsoni Tanganyika Yeh Liang-Sheng,
present paper.

Gazellostrongylus gen. nov.

Gazellostrongylus lerouxi sp. nov.

G. thomsoni Tanganyika Yeh Liang-Sheng,
present paper.

Filariidae (Cobbold, 1864) Claus, 1885.

Gazellofilaria Yeh Liang-Sheng, 1955.

Gazellofilaria tanganyikae Yeh Liang-Sheng, 1955.

G. thomsoni Tanganyika Yeh Liang-Sheng, 1955.

SUMMARY.

The present paper is a report on a collection of helminths collected from gazelles from Tanganyika Territory. It comprises one species of trematode, *Paramphistomum microbathrium*; one species of a larval cestode *Taenia hydatigena*; eleven species of nematodes, *Trichuris spiricollis*; *Haemonchus contortus*; *Trichostrongylus probolurus*; *Gazellofilaria tanganyikae*; *Cooperioides antidorca*; *Paracooperia serrata*; *P. daubneyi*; *Longistrongylus meyeri*; *Impalaia nudicollis*;

Gazellostrongylus lerouxi gen. et sp. nov. (Trichostrongylidae) and *Protostrongylus gazellae* sp. nov. The seven last mentioned species are all new records for the gazelle.

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